

THERMAL RESISTANCE AND ACCLIMATION RATE IN YOUNG WHITE AND BROWN
SHRIMP, *Penaeus setiferus* LINN. AND *Penaeus aztecus* IVES

by

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November 1975

TAMU-SG-76-202

Partially supported through Institutional Grant 04-3-158-18
to Texas A&M University
by the National Oceanic and Atmospheric
Administration's Office of Sea Grants
Department of Commerce,
and by
Texas Agricultural Experiment Station Project No. 4011,
Department of Wildlife and Fisheries Sciences
Texas A&M University.

\$4.00

Order from:

Department of Marine Resources Information
Center for Marine Resources
Texas A&M University
College station, TX 77843

ABSTRACT

Thermal Resistance and Acclimation Rate in Young White
and Brown Shrimp, *Penaeus setiferus* LINN. and
Penaeus aztecus IVES.

Penaeus aztecus postlarvae acclimated at three temperatures (24, 29, and 34 C) were tested for thermal resistance at five lethal temperatures for each acclimation temperature (34-38 C; 35-39 C; and 36-40 C). *Penaeus setiferus* postlarvae acclimated at two temperatures (29 and 34 C) were tested for thermal resistance at six lethal temperatures for each acclimation temperature (35-40 C; 36-41 C). The temperature which caused 50% mortality at 10,000 minutes was between 35 and 36 C for postlarvae acclimated at 24 C, and between 36 and 37 C for those acclimated at 29 and 34 C. Twenty-four hour LC_{50} 's were 36.3, 37.5, and 38.3 C for *Penaeus aztecus* postlarvae acclimated at 24, 29, and 34 C, respectively, and 38.3 and 38.9 for *Penaeus setiferus* postlarvae acclimated at 29 and 34 C, respectively.

Postlarval *Penaeus aztecus* were more resistant at most lethal temperatures than were 30 mm *Penaeus aztecus*. Postlarval and 30 mm *Penaeus setiferus* had similar resistance times, which were greater than those of 50 mm *Penaeus setiferus*.

Most of the acclimation of *Penaeus aztecus* postlarvae to a 5 C increase (25-30 C) and a 9 C increase (25-34 C) in temperature was completed in 3-4 days. Acclimation to the 5 C increase in temperature continued for 14 to 22 days after the transfer to 30 C. Postlarvae subjected to the 9 C increase tended to overshoot the new acclimation level for 4-6 days after transfer to 34 C. *Penaeus aztecus* postlarvae completed most of their acclimation to a 5 C decrease (29 to 24 C) in temperature in 2 days, but complete acclimation required over 21 days.

Penaeus setiferus postlarvae completed acclimation to a 5 C increase (29 to 34 C) in temperature in 1 day, whereas acclimation to an 8 C increase (27 to 35 C) required 2 days. *Penaeus setiferus* postlarvae completed most of their acclimation to a 5 C decrease (29 to 24 C) in temperature in 3 days, but acclimation was not complete even after 22 days.

Penaeus aztecus postlarvae, which enter the bays in the spring, when temperatures are mild, have less thermal resistance and a slower rate of acclimation to a temperature increase than do *Penaeus setiferus* postlarvae which enter in the summer.

Separate groups of *Penaeus setiferus* and *Penaeus aztecus* postlarvae were acclimated at the six combinations of two temperatures (29 and 34 C) and three acclimation salinities (25, 35, and 45 ppt), and tested for thermal resistance at each of the six combinations of three test salinities (25, 35, and 45 ppt) and two lethal temperatures. Thermal resistance was greatest at a test salinity of 25 ppt,

but an acclimation salinity of 45 ppt proved to be the best preparation for thermal resistance at all test salinities.

Penaeus setiferus postlarvae were acclimated at the six combinations of two temperatures (29 and 34 C) and three salinities (5, 15, and 25 ppt) and tested at the six combinations of three test salinities (5, 15, and 25 ppt) and two lethal temperatures. Thermal resistance was greatest at a test salinity of 25 ppt, but an acclimation salinity of 5 ppt was the best preparation for thermal resistance at all test salinities.

A test salinity of 25 ppt was the most favorable for resisting lethal temperatures in all experiments. However, acclimation to a higher or lower salinity gave maximum protection against heat death at that salinity and at all salinities closer to 25 ppt. In both species, 25 ppt is the test salinity closest to the isosmotic salinity (28-30 ppt) reported for larger shrimp (>100 mm). Therefore, thermal resistance appears to be greatest at salinities near the isosmotic salinity of both species. Good thermal resistance at all test salinities after acclimation to hyper- or hypoosmotic levels may be an adaptation allowing postlarvae of both species to resist high temperatures in hyper- or hyposaline bays.

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INTRODUCTION

The brown shrimp, *Penaeus aztecus*, and the white shrimp, *Penaeus setiferus*, are estuarine animals of great commercial importance which support a major fishery in the northern Gulf of Mexico (Farfante, 1969). The great demand for shrimp, the fluctuating yields of the shrimp fishery, and the present interest in shrimp mariculture, contribute to the practical need for knowledge of the physiology and ecology of these two species.

Knowledge of the limits of temperature tolerance, of the effect of salinity on temperature tolerance, and of the ability of an estuarine organism to adjust to changes in temperature can be important to an understanding of the physiology and ecology of that organism. Information on the limits of temperature tolerance is important because extremes of temperature may prove fatal to the organism (Brett, 1956). Variations in salinity may modify the effects of temperature on the organism (Wiesepape, Aldrich and Strawn, 1972); therefore, a study of the effect of salinity on temperature tolerance may be important in determining the temperature tolerance limits of the organism.

Changes in environmental temperature may cause the organism to adjust its metabolism in order to operate efficiently at the new temperature (Bullock, 1955). A knowledge of the rate of adjustment

The citations on the following pages follow the format of the journal "Transactions of the American Fisheries Society."

is necessary in order to determine the effects of changes in temperature on the organism. Increasing use of estuaries as sites for power plants, and the release of heated effluents by these plants into the estuary, raise questions about the effects of these plants on estuarine organisms (Mihursky and Kennedy, 1967). Information on the thermal tolerance and acclimation rate of an estuarine organism could be helpful in evaluating the effects of a power plant on that organism.

The successful culture of an organism requires a knowledge of the effects of environmental factors upon that organism. Information on the temperature tolerance and acclimation rate of the organism are useful in determining what temperature conditions are necessary for the culture of the organism.

The purpose of this investigation was to obtain information on the thermal tolerance, acclimation rate, and effects of salinity on thermal resistance in postlarval brown and white shrimp. The investigation was undertaken in order to provide information which could be useful in shrimp mariculture and in evaluation of the ecology of the two species.

Poikilothermal animals are able to function normally within a certain range of temperatures, which is termed the "zone of tolerance" (Brett, 1956). Higher temperatures, which are fatal for at least 50% of a population, are termed lethal temperatures and constitute the "zone of resistance" (Brett, 1956). The boundary between the two zones is difficult to define, as animals may die, apparently

from temperature effects, for weeks after introduction into a high temperature (Gibson, 1954).

Some authors define the difference between lethal and non-lethal temperatures in terms of an "upper incipient lethal temperature" below which the test animals will live for an indefinite period of time (Brett, 1956; Fry, 1957). However, since the lethal effects of temperature may extend over a considerable period of time, the definition of an "indefinite period of time" is difficult (Gibson, 1954; Sprague, 1963). In view of this, it is perhaps more accurate to define lethal temperature in terms of a definite period of time, as suggested by Orr (1955). This is often termed the LC_{50} , or level of temperature which will kill 50% of a sample in a specified period of time (Sprague, 1963).

Many investigators define the results of thermal resistance experiments in terms of a test period of 10,000 minutes. Examples are the studies on the fishes *Lebistes reticulatus* (Gibson, 1954) and *Ictalurus punctatus* (Allen and Strawn, 1967). Most reports of upper incipient lethal temperatures are based on test periods of 10,000 minutes; therefore, these often correspond to 10,000 minute LC_{50} 's.

Reports of 24-hour (1440 minute) LC_{50} 's are also common. Sprague (1963) reported the results of his study of thermal resistance in four species of freshwater crustaceans in terms of a 24-hour LC_{50} . This method was also used by Kennedy and Mihursky (1971) in reporting on the thermal resistance of three species of estuarine bivalves.

The time from introduction into the lethal temperature until the death of the organism is termed the resistance time, and is affected by the level of the lethal temperature (Brett, 1956). Generally, resistance time at high temperatures increases with decreasing lethal temperature (Fry, 1957).

Many investigations of the thermal resistance of fishes at high lethal temperatures have been conducted. Fry, Brett and Clawson, (1942) studied the effects of high lethal temperatures on the goldfish, *Carassius auratus*. Similar studies were conducted on *Girella nigricans*, *Fundulus parvipinnis*, and *Atherinops affinis* by Doudoroff (1942, 1945). Other species of fishes studied include: *Catostomus commersoni*, *Rhinichthys stratulus*, *Semotilus atromaculatus*, *Pimephales promelas*, *Notropis cornutus*, *Notropis atherinoides*, and *Perca flavescens* (Hart, 1947); *Rutilus rutilus* (Cocking, 1959); *Menidia menidia*, *Pseudopleuronectes americanus*, and *Spheroides maculatus* (Hoff and Westman, 1966); *Coregonus artedii* (Edsall and Colby, 1970); and *Notropis pilsbryi* and *Lepomis macrochirus* (Hickman and Dewey, 1973). Several species of molluscs have also been tested for thermal resistance at high lethal temperatures. These include: *Modiolus demissus* (Waugh, 1972); *Mya arenaria*, *Macoma balthica*, *Mulina lateralis*, and *Gemma gemma* (Kennedy and Mihursky, 1971). Similar studies have been conducted on some echinoderms (Farmanfarmaian and Giese, 1963; Singletary, 1971). Investigations of thermal resistance at high lethal temperatures have also been conducted on crustaceans: *Orconectes rusticus* (Spoor, 1955); *Homarus americanus* (McLeese, 1956);

Astacus pallipes (Bowler, 1963); *Mysis relicta* (Smith, 1970); *Gammarus lacustris* (Smith, 1973); *Asellus intermedius*, *Hyalella azteca*, *Gammarus fasciatus*, and *Gammarus pseudolimnaes* (Sprague, 1963); and *Callinectes sapidus* (Holland, Aldrich and Strawn, 1971).

The previous thermal history (or acclimation temperature) may also influence resistance time (Fry, 1957). Animals acclimated at lower temperatures generally have shorter resistance times than those from higher temperatures, at a given high lethal temperature (Gibson, 1954; Neill, Strawn and Dunn, 1966; Allen and Strawn, 1967).

The effect of acclimation temperature on thermal resistance, like the effect of lethal temperature, has been reported for many species of animals from several phyla. These include fishes (Doudoroff, 1942 and 1945; Fry *et al.*, 1942; Hart, 1947; Cocking, 1959; Hoff and Westman, 1966; Edsall and Colby, 1970; Hickman and Dewey, 1973), molluscs (Waugh, 1972; Kennedy and Mihursky, 1971), echinoderms (Farmanfarmaian and Giese, 1963; Singletary, 1971), and crustaceans (Spoor, 1955; McLeese, 1956; Bowler, 1963; Sprague, 1963; Smith, 1970, 1973; Holland *et al.*, 1971).

Individual organisms of the same species have different resistance times when exposed to a lethal temperature (Fry, 1957). The exact reasons for these differences are not well known, although several theories have been proposed. Hoar and Cottle (1952) suggest that differences in the lipids fed to animals cause differences in resistance time. Ushakov (1964) reviewed the work relating lipid composition to thermal death, and found that there were many cases

where lipid composition could not explain differences in resistance time. Christophersen and Precht (1953) proposed the theory that changes in the water content of the cells results in differences in thermal resistance. Fry (1958) challenged this theory on the grounds that not all differences in thermal resistance may be explained by differences in the water content of the cells. Denaturation of proteins in cells has also been proposed as the cause of thermal death; however, as Read (1964) and Ushakov (1964) point out, denaturation usually occurs at temperatures well above those which cause the death of the whole organism. Bowler (1963b) suggested that heat death was due to loss of nervous co-ordination due to an imbalance in blood sodium and potassium, which in turn was caused by a breakdown of the cation pump mechanism of the tissues. Biochemical changes in the cells of the organism have also been suggested as possible causes of thermal death (Prosser, 1967).

Gibson (1954), in a study of the thermal resistance of *Lebistes reticulatus*, suggested that there was more than one cause of death (or lethal effect) at some lethal temperatures. Tyler (1966) also noted the presence of different lethal effects in *Chrosomus eos* and *C. neogaeus*, as did Allen and Strawn (1967) in *Ictalurus punctatus*. Neill et al. (1966) suggested that high variance among logarithms of the resistance times of an experimental population indicated that multiple lethal effects were involved. Thus, high variance was thought to be an indication of the presence of different lethal effects, or physiological death mechanisms. The causes of these

lethal effects have not been determined.

Fry (1957) found that resistance time may vary between different species, as well as between individuals within the species. He has suggested that these differences might be used to define the differences between species. Differences between species have been reported by Hart (1947), Doudoroff (1945), Hoff and Westman (1966), Sprague (1963), Kennedy and Mihursky (1971), and Singletary (1971).

Differences in thermal resistance may also exist between species from the same genus. Tyler (1966) reported differences in thermal resistance between two species of *Chrosomus*, and Todd and Dehnel (1960) found differences in thermal resistance between two species of *Hemigrapsus*. Differences in thermal resistance were also reported for two species of *Gammarus* (Smith, 1973).

Resistance to lethal temperatures may also vary with the life stage of the organism. Brett (1960) reported that in pacific salmon, the upper limits of survival varied between eggs, fry, and adults. Differences in thermal resistance at different life stages were also reported for *Salmo salar*, *Salmo trutta trutta*, and *Salmo trutta fario* (Spass, 1960).

Seasonal variations in thermal resistance have been reported in some species. Hoar (1955) reported differences in thermal resistance between summer and winter goldfish, *Carassius auratus*. Similar results were reported by Todd and Dehnel (1960) for *Hemigrapsus oregonensis* and *H. nudus*. Tyler (1966) also reported differences in thermal resistance between summer and winter *Chrosomus eos* and *C.*

neogaeus. Sprague (1963) found, however, that *Asellus intermedius* collected in different seasons of the year did not vary appreciably in their thermal resistance. Roberts (1957) also reported that *Pachygrapsus crassipes* did not differ in oxygen consumption at different times of the year.

Poikilotherms are able to adapt to changes in their environmental temperature, a process referred to as acclimation or acclimatization. The terms acclimation and acclimatization have been used interchangeably by some authors (Bullock, 1955; Kinne, 1967). The definition I use was proposed by Fry (1958), who defined acclimation as the day to day adjustments to temperature by an individual organism, and acclimatization as long-term, seasonal adjustments to temperature.

Animals acclimated at different temperatures sometimes exhibit physiological differences (Bullock, 1955) which can be used to study the process of acclimation. Among the most commonly used characteristics are changes in oxygen consumption (Grainger, 1956; Roberts, 1957; Vernberg, 1959) and changes in thermal resistance at a given lethal temperature (Bowler, 1963a, Sprague, 1963; Allen and Strawn, 1971).

Differences in oxygen consumption at different temperatures have been reported in several species of animals (Kinne, 1963). In general, oxygen consumption seems to increase with increasing acclimation temperature (Grainger, 1956; Vernberg, 1959; Carlisle and Cloudsley-Thompson, 1968).

Thermal resistance time, at a given lethal temperature, increases with increasing acclimation temperature (Fry, 1957). This fact can be used to determine the rate of acclimation to a change in temperature (Loeb and Wasteneys, 1912). The method normally used to determine acclimation rate is to allow animals to acclimate to a certain temperature, then transfer them to a new acclimation temperature which is higher or lower than the original temperature. Animals from the test population are tested for thermal resistance at a lethal temperature just before transfer to the new acclimation temperature (to determine thermal resistance time of animals held at the original acclimation temperature) and at periodic intervals after transfer to the new acclimation temperature. Since thermal resistance time at the new acclimation temperature will differ from resistance time at the original acclimation temperature, resistance time should change until the animals become acclimated to the new temperature. After the organisms have become acclimated to the new acclimation temperature, the resistance time should stabilize at a level consistent with the new temperature.

Many organisms complete most of their adjustment to an increase in temperature in 1-3 days. Loeb and Wasteneys (1912) reports that *Fundulus* acclimated to a 2 C increase in temperature in 30 hours. *Girella nigricans* transferred from 14 C to 26 C completed acclimation in 1 day (Doudoroff, 1942). *Orconectes rusticus* also completed acclimation to a temperature increase (4 C to 22-26 C) in 1 day (Speer, 1955). Sprague (1963) found that *Asellus intermedius* completed

acclimation to an 8 C temperature increase in 3 days, while *Hyalella azteca* and *Gammarus fasciatus* required 2 days. *Astacus pallipes* required approximately 3 days to acclimate to 25 C after being transferred from 8 C (Bowler, 1963a). Allen and Strawn (1971) reported that *Ictalurus punctatus* completed most of its acclimation to different increases in temperature in 1-3 days. McLeese (1956) found that acclimation to a 8 C temperature increase took 22 days in *Homarus americanus*.

Loss of thermal resistance after a decrease in acclimation temperature may take longer than acclimation to an increase in temperature. Loeb and Wasteneys (1912) found that *Fundulus* acclimated at 27 C did not lose thermal resistance even after 33 days at 14 C. *Girella nigricans* took 34 days to reacclimate after a change from 26 to 14 C (Doudoroff, 1942). In *Orconectes rusticus*, acclimation to 4 C after transfer from 22-26 C required at least 16 days (Speer, 1955). *Ictalurus punctatus* required from 4 to 15 days to acclimate to decreases in temperature (Allen and Strawn, 1971).

Several environmental factors have been found to affect thermal resistance in poikilotherms. Salinity is one such factor which may act to modify the effects of temperature on marine animals (Kinne, 1967). Loeb and Wasteneys (1912) found that some salts in the water improved the thermal resistance of *Fundulus*. Strawn and Dunn (1967) also found that some salts in the water increased the thermal resistance of 10 species of marsh fishes that they tested. Optimum thermal resistance in an isosmotic medium, and a progressive reduction of

thermal resistance at higher and lower salinities has been reported for *Fundulus heteroclitus* and *Fundulus diaphanes* (Garside and Jordan, 1968), and *Fundulus kansae* (Hill and Carlson, 1970). McLeese (1956) found that lower salinities caused a reduction in the upper lethal temperature of the American lobster (*Homarus americanus*). Thermal resistance increased with increasing salinity in the copepod *Tigriopus fulvus* (Ranade, 1957). Todd and Dehnelt (1960) also found that thermal resistance was greater at higher salinities in the grapsoid crabs *Hemigrapsus nudus* and *Hemigrapsus oregonenses*. The blue crab, *Callinectes sapidus*, also showed increasing thermal resistance with increasing salinity (Tagatz, 1969). Lewis and Hettler (1968), however, found that salinity did not markedly affect survival at high temperatures in the menhaden, *Brevoortia tyrannus*.

Brown shrimp (*Penaeus aztecus*) and white shrimp (*Penaeus setiferus*) are the two most common penaeid shrimps along the upper Texas Coast. Both species enter the bays as postlarvae, and remain there during their development into adults (Farfante, 1969). The majority of brown shrimp postlarvae enter the bays in the early spring (March to May), with smaller numbers entering throughout the summer and early fall. White shrimp postlarvae first appear in the bays in late spring (May and June) and continue to enter throughout the summer and early fall (Baxter and Renfro, 1966).

Mock (1966) found that postlarval brown shrimp are most abundant in the shallow areas of the bay, next to the shoreline. Parker (1970) also found that the smallest brown shrimp were located in the

peripheral and shore areas of the bays.

Gunter (1956, 1961) found that postlarval brown and white shrimp were able to enter areas of very low salinity, and concluded that low salinity was necessary for the survival of both species. Parker (1970) also found that young brown shrimp were present in waters of very low salinity, but concluded that salinity *per se* had no effect on distribution. Gunter, Christmas and Killebrew (1964) found that young white shrimp were generally more prevalent at lower salinities than young brown shrimp, and concluded that white shrimp were more tolerant of low salinities than were brown shrimp.

Zein-Eldin (1963) found that salinity over a broad range (2-40 ppt) did not adversely affect growth and survival of postlarval penaeid shrimp (primarily *P. aztecus*) at moderate temperatures (24.5-26 C). Zein-Eldin and Aldrich (1965) also reported that salinity had little effect on growth and survival of postlarval *Penaeus aztecus* over a wide range of temperature. They did find, however, that temperatures below 15 C reduced the tolerance of the postlarvae to lower (less than 15 ppt) salinities. Zein-Eldin and Griffith (1969) found that postlarval white shrimp were also able to tolerate a wide range of salinities (2-40 ppt), except at extreme low temperatures (less than 15 C).

McFarland and Lee (1963) found that both white and brown shrimp (size = >100 mm) were able to regulate their internal osmotic concentrations to some extent. Both species were isosmotic to salinities of 27.6-28.3 ppt. At salinities below 27.6 ppt both species

maintained internal concentrations greater than that of the medium. At salinities above 28.3 ppt, both species maintained internal concentrations less than that of the medium. They reported that white shrimp are better regulators at salinities below the isosmotic salinities, but that brown shrimp are better regulators at salinities above the isosmotic salinities.

A previous investigation (Wiesepape *et al.*, 1972) gave some limited information on the thermal tolerance, acclimation rate, and effect of salinity on thermal resistance in postlarval brown shrimp. It was found that the salinity at which the postlarvae were acclimated, and the salinity at which a lethal temperature was experienced, influenced their resistance time. Reduced salinities in the lethal baths reduced thermal resistance, while low acclimation salinities usually provided a better preparation for resisting lethal temperatures at any salinity; however, the salinities used by Wiesepape *et al.* covered only the lower range of salinities that the shrimp might encounter. An investigation of the effects of salinities above the isosmotic salinity of brown shrimp is needed to give a complete picture of the effects of salinity on thermal resistance of this species.

The experiments on thermal resistance and acclimation rate conducted by Wiesepape *et al.* were designed to provide information for their temperature-salinity study, and therefore they did not study the effects of a wide range of temperatures on thermal resistance, or of different temperature changes on acclimation. Investigation of thermal resistance at a wider range of lethal temperatures is necessary

in order to understand the upper temperature tolerances of brown shrimp. A study of the acclimation rate of brown shrimp to different increases in temperature, as well as to decreases in temperature, is also necessary in order to obtain a better idea of the acclimation of this species to temperature changes.

No studies of the type conducted by Wiesepepe *et al.* (1972) have been conducted on white shrimp. An investigation of temperature tolerance, acclimation rate, and effect of salinity on thermal resistance of this species would also be useful. A comparison of thermal resistance and acclimation in brown and white shrimp could also help in understanding the relationship of the two species. As a result, the specific purposes of the present investigation are to study further the temperature tolerance and acclimation rate in brown shrimp, to conduct similar studies on white shrimp, and to compare observed results for the two species.

MATERIALS AND METHODS

General Procedures

Three different studies were conducted on both white and brown shrimp:

- 1) In the thermal resistance experiments, shrimp were held at two (or three) different acclimation temperatures for 6 days. Samples from each acclimation temperature were then tested at five different lethal temperatures to determine the resistance time of the individual shrimp.
- 2) In the acclimation experiments, shrimp were held at an acclimation temperature for 6 days, then transferred to an acclimation temperature which was higher or lower than the original temperature. Samples of ten shrimp from each temperature change were tested for thermal resistance at a lethal temperature at intervals after the acclimation temperature change to determine the rate of acclimation to the new temperature.
- 3) The temperature-salinity experiments consisted of acclimating shrimp at the six possible combinations of two acclimation temperatures and three acclimation salinities. Samples of ten shrimp from each acclimation combination were then tested for thermal resistance at the six combinations of two lethal temperatures and three test salinities.

Postlarvae undergoing acclimation were fed brine shrimp nauplii daily to maintain a population of nauplii in the tanks at all times during acclimation. Larger shrimp were fed Tetramin fish food (Tetra Sales Corp.) twice daily to provide 25% of the estimated weight of the shrimp in the tank during acclimation. Shrimp being tested for thermal resistance in the acclimation and temperature-salinity experiments were not fed during the tests. In the thermal resistance experiments, shrimp surviving over 1,000 minutes were fed twice daily for the duration of the experiment.

In all of the thermal resistance tests, the shrimp were watched continuously for the first 100 minutes, and checked at intervals thereafter. The intervals were chosen so as to avoid an error of more than 5% in the observed death time (i.e., 5 min. at 100 min.; 50 min. at 1,000 min.; etc.). All tests were terminated at 10,000 minutes, even though there were shrimp surviving at that time.

Cessation of coordinated appendage movement (thoracic limbs and pleopods) was used as the indication of death. In larger shrimp, I observed that cessation of appendage movement correlated well with the termination of respiration, as indicated by cessation of the beating of the scaphognathite.

In both acclimation and lethal test tanks, the desired salinity was obtained by adding either distilled water or Instant Oceans Sea Salts to Gulf of Mexico seawater. Salinity was determined with a Goldberg refractometer (American Optical Co.). Temperature and salinity were checked daily, and evaporated water was replaced with

distilled water.

Postlarvae for this investigation were collected at three sites near Galveston Island. Station 1 was located on the beach near the 61st street fishing pier, station 2 in the entrance to Galveston Bay, west of south jetty, and station 3 on the Gulf side of the south jetty (Fig. 1). The source of postlarvae for a particular experiment depended on availability, since they were often present at one station and not at the others. The postlarvae were captured using a hand drawn beam trawl as described by Renfro (1962).

Juvenile brown shrimp were raised in the laboratory from postlarvae captured for the thermal resistance experiments. Juvenile white shrimp were obtained from the National Marine Fisheries Service Biological Laboratory in Galveston, Texas (NMFS).

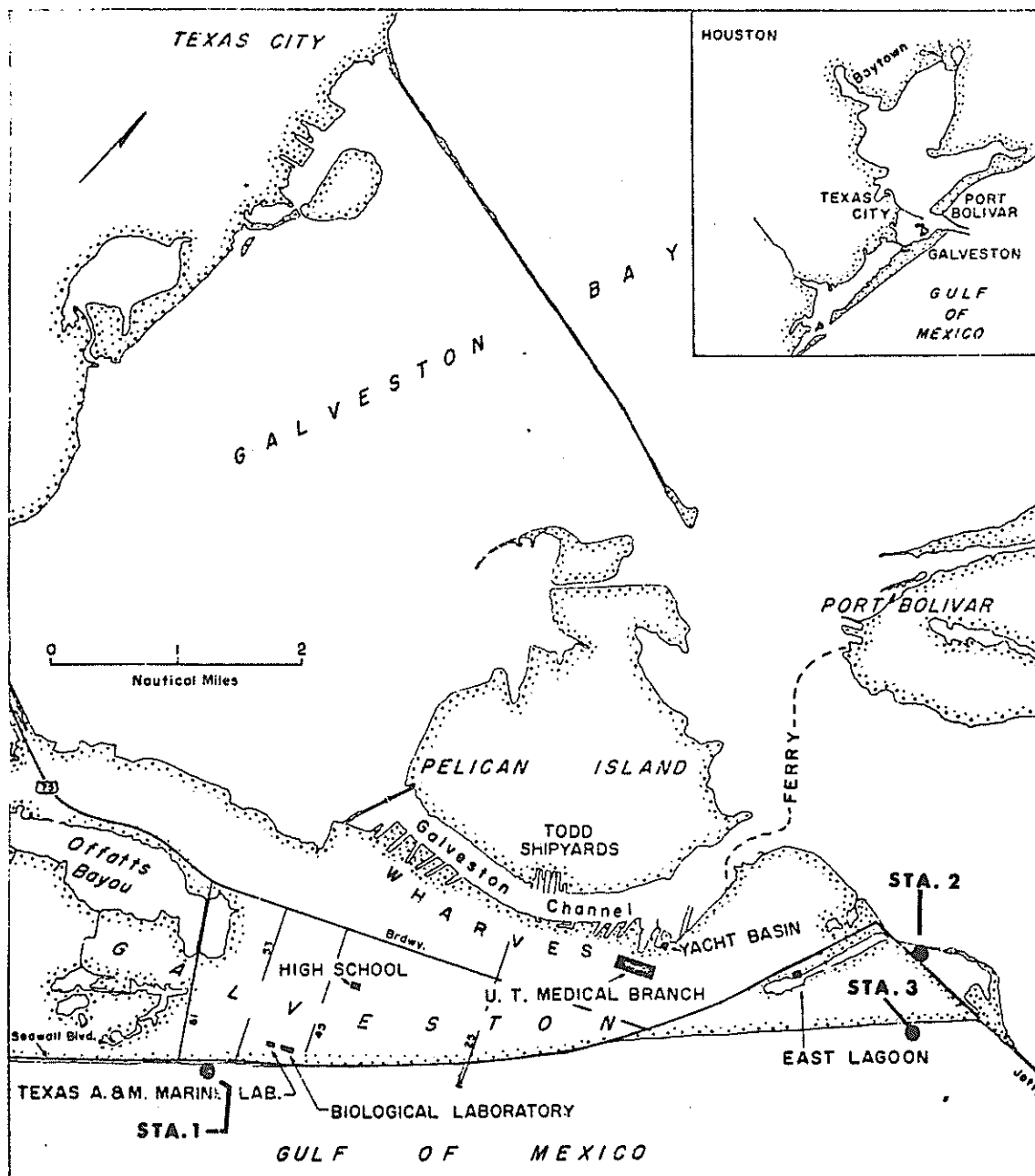
Equipment

Acclimation Equipment

In the thermal resistance and acclimation experiments, the shrimp were acclimated in enclosed, insulated 333 l acclimation tanks constructed of plywood covered with polyester resin. In the temperature-salinity experiments, shrimp were acclimated in 22.7 l glass aquaria placed in the acclimation tanks, which served as water baths.

Temperature in the acclimation tanks was controlled by an electrical relay which was activated by a contact thermometer. When the desired acclimation temperature was above room temperature, the relay

FIGURE 1.--Map of Galveston, Texas, area showing the locations of the three stations at which postlarvae were collected (black circles).



activated a 250 W aquarium heater. For temperatures below room temperature, the relay activated a cooling coil in the tank. Air stones in the tank, and in the aquaria in the temperature-salinity experiments, aerated and circulated the water to prevent thermal stratification. It was possible to maintain the temperature in the acclimation tanks to within ± 0.1 C of the desired temperature with this system. Each acclimation tank (or aquarium) was equipped with an undergravel filter which was covered with crushed oyster shell. This type of filter has been found to be effective in converting ammonia into less toxic forms (King, 1973). A Tork Model 7300 timer controlled a 30 W Standard Cool White fluorescent bulb in each tank. The timers were set to provide a photoperiod of 12 hours of light and 12 hours of darkness in all experiments.

Lethal Test Equipment

The thermal resistance tests were conducted in 30 l lethal test tanks, constructed of polyester resin-covered plywood. One end of these tanks, and the top, consisted of a sheet of plexiglas. Temperature in these tanks was controlled in the same manner as in the acclimation tanks, except that no cooling system was present. Two air stones in each tank aerated and circulated the water. Each tank had an undergravel filter covered with crushed oyster shell.

Postlarvae were placed inside small cages during the thermal resistance tests to keep them within easy view of the observer. These cages were constructed of plexiglas of 6.35 or 12.7 mm thickness

with plastic window screen on two sides to allow water circulation. A 12.5 mm opening in the top allowed access and was closed with a 00 rubber stopper. The outside measurements of the cages were approximately 5.0 x 5.0 x 2.5 cm. Five cages were placed in a plexiglas holder which facilitated transfer of the postlarvae to the lethal test tanks. Inside the tanks, the holders were placed on a plexiglas rack. The larger (30 and 50 mm) shrimp were not confined in cages, but were placed directly in the lethal test tanks.

Specific Procedures

Thermal Resistance Experiments

In all of these experiments, there were two replications of all acclimation and test conditions, the shrimp were acclimated for 6 days prior to the thermal resistance tests, and a salinity of 25 ppt was used in all acclimation and test tanks.

Brown shrimp postlarvae.--Postlarvae for this experiment were collected at station 1 (Table 1). One hundred and fifty postlarvae were placed in each of six acclimation tanks of which two tanks were held at 24 C, two at 29 C, and two at 34 C (Table 2). Twenty postlarvae from each acclimation tank were tested for thermal resistance at five lethal temperatures (Table 2, p. 23).

White shrimp postlarvae.--Postlarvae for this experiment were collected at station 1 (Table 1, p. 22). One hundred and fifty postlarvae were placed in each of four acclimation tanks of which two

TABLE 1.--Date and station of collection, and water temperature and salinity at the time of collection, for postlarvae used in all experiments.

Experiment	Date	Station	Water temperature (C)	Salinity (ppt)
Thermal resistance experiments				
Brown shrimp postlarvae	4/2/73	1	20	22
White shrimp postlarvae	8/28/73	1	28	20
Acclimation experiments				
Brown shrimp postlarvae (A-H)	4/14/72	2	25	26
Brown and white shrimp postlarvae (I-IV)	8/28/73	1	28	20
White shrimp postlarvae (V-VI)	8/6/73	3	27	33
White shrimp postlarvae (VII-VIII)	7/19/73	1	30	33
White shrimp postlarvae (IX-X)	7/29/69	1	28	24
Temperature-salinity experiments				
Brown shrimp postlarvae, high salinity	5/6/73	3	25	13
White shrimp postlarvae, low salinity	9/10/73	3	29	33
White shrimp postlarvae, high salinity	7/15/73	3	28	20

TABLE 2.--*Lethal temperatures used in the thermal resistance tests on brown shrimp postlarvae.*

	Acclimation temperature (C)		
	24	29	34
	34		
	35	35	
Lethal temperatures	36	36	36
	37	37	37
	38	38	38
		39	39
			40

tanks were held at 29 C and two at 34 C (Table 3). Twenty postlarvae from each acclimation tank were tested for thermal resistance at six lethal temperatures (Table 3, p. 25).

Species comparison.--Brown shrimp postlarvae, collected at the same time as the white shrimp postlarvae, were placed in four acclimation tanks having the same temperatures as those containing the white shrimp postlarvae (Table 3, p. 25). Twenty postlarvae from each acclimation tank were tested at three lethal temperatures at the same time as were the white shrimp postlarvae (Table 3, p. 25).

30 mm brown shrimp.--Brown shrimp used in this experiment were raised from postlarvae at 22 C in the laboratory. They were acclimated in four acclimation tanks, of which two were held at 29 C and two at 34 C (Table 4). Twenty shrimp from each acclimation tank were tested at three lethal temperatures (Table 4, p. 26).

30 mm and 50 mm white shrimp.--White shrimp, which averaged 30 mm in total length, were obtained from the NMFS in September, 1972. They had been raised from eggs obtained from adult Gulf of Mexico white shrimp. The shrimp were held at 22 C and 24 ppt for 14 days prior to the start of the experiment. One hundred and thirty shrimp were placed in each of six acclimation tanks held at 24, 29, and 34 C. Twenty shrimp from each acclimation tank were tested at each of five lethal temperatures (Table 5).

White shrimp of 50 mm average total length, from the same population as the 30 mm shrimp, were obtained in November, 1972. They were acclimated to the same conditions as the 30 mm shrimp (Table 5, p. 27).

TABLE 3.--Lethal temperatures used in the thermal resistance experiment comparing white and brown shrimp postlarvae

	Brown shrimp		White shrimp	
	<u>Acclimation temperature</u>		<u>Acclimation temperature</u>	
	29	34	29	34
Lethal temperatures			35	
			36	36
	37		37	37
	38	38	38	38
	39	39	39	39
	40	40	40	40
				41

TABLE 4.--Lethal temperatures used in the thermal resistance tests on 30 mm brown shrimp.

	Acclimation temperature (C)	
	29	34
	37	37
Lethal temperatures	38	38
	39	39

TABLE 5.--Lethal temperatures used in the thermal resistance experiments on 30 and 50 mm white shrimp.

	30 mm			50 mm		
	Acclimation temperature			Acclimation temperature		
	24	29	34	24	29	34
Lethal temperature	34					
	35	35				
	36	36	36	36		
	37	37	37	37	37	
	38	38	38	38	38	38
		39	39		39	39
			40			40

Twenty shrimp from each acclimation tank were tested at each of three lethal temperatures (Table 5, p. 27).

Acclimation Experiments

In all of these experiments, there were two replications of all acclimation and test conditions, the shrimp were acclimated for 6 days prior to the thermal resistance tests, and a salinity of 25 ppt was used in all acclimation and test tanks. Lethal temperatures were chosen so as to give resistance times of less than 1,000 minutes.

Brown shrimp postlarvae.--Postlarvae for this experiment were collected at station 3 (Table 1, p. 22). One hundred and seventy-five postlarvae were placed in two tanks (tanks A&B) held at 25 C, and in two tanks at 29 C (tanks G&H). Three hundred postlarvae were placed in each of four tanks held at 25 C (tanks C, D, E, and F) (Table 6).

After 6 days of acclimation, the shrimp in tanks A, B, C, and D were transferred to two acclimation tanks at 30 C, the postlarvae in tanks E and F were transferred to two tanks at 34 C, and the postlarvae in tanks G and H were transferred to two tanks at 24 C (Table 6, p. 29). Thus, different groups of postlarvae underwent a 5 C (25 to 30 C) increase (tanks A-D), a 5 C (29 to 24 C) decrease (tanks G&H), and a 9 C (25 to 34 C) increase (tanks E&F) in acclimation temperature (Table 6, p. 29).

Ten postlarvae from tanks A&B, undergoing a 5 C increase in acclimation temperature, were tested for thermal resistance at 38.7 C at just before transfer to 30 C and at 3, 12 and 24 hours after transfer.

TABLE 6.--Changes in acclimation temperature, lethal temperature, and test intervals used in the acclimation experiment on brown shrimp postlarvae

	Holding (acclimation) tank			
	A&B	C&D	E&F	G&H
First holding temperature (C):	25.0	25.0	25.0	29.0
Second holding temperature (C):	30.0	30.0	34.0	24.0
Lethal temperature:	38.7	38.3	39.5	38.5
Thermal resistance test schedule (days after transfer to second holding temperature):	0	0	0	0
	0.125	0.125	0.125	0
	0.5	0.5	0.5	0
	1	1	1	1
	2	2	2	2
	3	3	3	3
	4	4	4	4
	5	5	5	5
	6	6	6	6
	7	7	7	7
	8	8	8	8
	9	9	9	9
	10	10	10	10
	11	-	-	11
	12	12	12	12
	13	-	-	13
	14	14	14	14
	15	-	-	15
	16	-	-	-
	-	-	-	17
	18	-	-	-
	-	-	-	19
	20	-	-	-
	-	-	-	21
	22	-	-	-

After 24 hours, ten postlarvae from each tank were tested at 1-day intervals to 16 days, and thereafter at 2-day intervals to 22 days (Table 6, p. 29).

The other postlarvae undergoing a 5 C (25 to 30 C) increase in acclimation temperature, tanks C&D, were tested at 38.3 C using ten shrimp per test, at just before transfer to 30 C and at 3, 12, and 24 hours after transfer. After 24 hours they were tested at 1-day intervals to 10 days, and thereafter at 2-day intervals to 14 days (Table 6, p. 29).

The postlarvae undergoing a 9 C increase in acclimation temperature (tanks E&F) were tested at 39.5 C at just before transfer to 34 C and at 3, 12, and 24 hours after transfer. After 24 hours, they were tested at 1-day intervals to 10 days, and at 2-day intervals to 14 days (Table 6, p. 29).

The postlarvae undergoing a 5 C decrease in acclimation temperature, tanks G&H, were tested at 38.5 C at just before transfer to 24 C, and at 1-day intervals to 15 days. They were then tested at 2-day intervals to 21 days (Table 6, p. 29).

White shrimp postlarvae.--It was impossible to conduct this entire experiment at one time, because white shrimp postlarvae were never available in sufficient numbers. Therefore, postlarvae for these tests were collected at different times during July and August, 1973.

White shrimp postlarvae for the experiment on acclimation to a 5 C increase in temperature were collected at station 1 (Table 1, p. 22).

Four hundred postlarvae were placed in each of two acclimation tanks at 29 C (tanks I&II). After 6 days, these postlarvae were transferred to two tanks at 34 C (Table 7). Ten postlarvae from each tank were tested for thermal resistance at 40 C at just before transfer to 34 C, and at 3, 12, and 24 hours after transfer. They were then tested at 1-day intervals to 8 days, and thereafter at 2-day intervals to 22 days (Table 7, p. 32).

White shrimp postlarvae to be used for a study of acclimation to an 8 C increase in acclimation temperature were collected at station 3 (Table 1, p. 22). Three hundred postlarvae were placed in two tanks at 27 C (tanks V&VI). After 6 days they were transferred to two tanks at 35 C (Table 7, p. 32). Ten postlarvae from each tank were tested at 40 C at just before transfer to 34 C, and at 3, 12, and 24 hours after transfer. They were then tested at 1-day intervals to 8 days, and thereafter at 2-day intervals to 14 days (Table 7, p. 32).

White shrimp postlarvae for the comparison of the effects of lethal temperature on acclimation rate were collected at station 1 (Table 1, p. 22). One hundred postlarvae were acclimated in each of two acclimation tanks at 29 C for 6 days (tanks IX&X). They were then transferred to two tanks at 34 C (Table 7, p. 32). Ten postlarvae from each tank were tested at 39.3 C at just before transfer to 34 C, and at 3, 12, and 24 hours after transfer, and then at 2, 4, and 6 days after transfer (Table 7, p. 32).

White shrimp postlarvae for a study of acclimation to a 5 C decrease in temperature were collected at station 1 (Table 1, p. 22).

TABLE 7.--Changes in acclimation temperature, lethal temperatures, and test intervals used in the acclimation experiments on white shrimp postlarvae

	Holding (acclimation) tank				
	I & II	III & IV	V & VI	VII & VIII	IX & X
First holding temperature (C):	29.0	29.0	27.0	29.0	29.0
Second holding temperature (C):	34.0	34.0	35.0	24.0	34.0
Lethal temperature (C):	40.0	40.0	40.0	38.8	39.3
Thermal resistance test	0	0	0	0	0
schedule (days after transfer	0.125	0.125	0.125	-	0.125
to second holding temperature):	0.5	0.5	0.5	-	0.5
	1	1	1	1	1
	2	2	2	2	2
	3	3	3	3	-
	4	4	4	4	4
	5	5	5	5	-
	6	6	6	6	6
	7	7	7	-	-
	8	8	8	8	-
	-	-	-	-	-
	10	-	10	10	-
	-	-	-	-	-
	12	-	12	12	-
	-	-	-	-	-
	14	-	14	14	-
	-	-	-	-	-
	16	-	-	16	-
	-	-	-	-	-
	18	-	-	18	-
	-	-	-	-	-
	20	-	-	20	-
	-	-	-	-	-
	22	-	-	22	-

Three hundred postlarvae were acclimated in each of two tanks at 29 C for 6 days (tanks VII & VIII). They were then transferred to two tanks at 24 C (Table 7, p. 32). Ten postlarvae from each tank were tested at 38.8 C at just before transfer to 24 C, at 1-day intervals to 6 days, and thereafter at 2-day intervals to 22 days (Table 7, p. 32).

Species comparison.---Brown shrimp postlarvae for the comparison study were collected at the same time as were the white shrimp postlarvae which were used in this study of acclimation to a 5 C increase in temperature (white shrimp tanks I & II) (Table 1, p. 22). One hundred and ten of these postlarvae were placed in each of two acclimation tanks (tanks III & IV) and subjected to the same acclimation conditions as were the white shrimp postlarvae in tanks I & II (Table 7, p. 32). Ten brown shrimp postlarvae were tested at 40 C at just before transfer to 34 C, and at 3, 12, and 24 hours after transfer. They were then tested at 1-day intervals to 8 days (Table 7, p. 32).

Temperature-Salinity Experiments

In these experiments, there were two replications of each acclimation and test condition. During acclimation, each replicate was held in a separate aquarium inside the same acclimation tank. All postlarvae were acclimated for 6 days prior to the thermal resistance tests.

Brown shrimp postlarvae: high salinity.---Brown shrimp postlarvae for this experiment were collected at station 3 (Table 1, p. 22). Seventy postlarvae were placed in each of two aquaria in each of six

acclimation tanks. Both aquaria in each acclimation tank were at one of the six possible combinations of two acclimation temperatures and three acclimation salinities (Table 8). Ten postlarvae from each aquarium were tested for thermal resistance at each of six combinations of two lethal temperatures and three test salinities (Table 8, p. 35).

White shrimp postlarvae: low salinity.--White shrimp postlarvae for this experiment were collected at station 3 (Table 1, p. 22). Seventy postlarvae were placed in each of two aquaria in each of six acclimation tanks. Both aquaria in each acclimation tank were at one of the six possible combinations of two acclimation temperatures and three acclimation salinities (Table 9). Ten postlarvae from each replicate were tested for thermal resistance at each of the six combinations of two lethal temperatures and three test salinities (Table 9, p. 36).

White shrimp postlarvae: high salinity.--White shrimp postlarvae for this experiment were collected at station 3 (Table 1, p. 22). Seventy postlarvae were placed in each of two aquaria in each of six acclimation tanks. Both aquaria in each acclimation tank were at one of the six possible combinations of two acclimation temperatures and three acclimation salinities (Table 10). Ten postlarvae from each aquarium were tested for thermal resistance at each of the six combinations of two lethal temperatures and three test salinities (Table 10, p. 37).

TABLE 8.--Acclimation and test conditions used in the temperature-salinity experiment (high salinity range) on brown shrimp*

Acclimation conditions		Test conditions	
Temperature	Salinity	Temperature	Salinity
29.0	25	38.2	25
29.0	35	38.2	35
29.0	45	38.2	45
		39.0	25
		39.0	35
		39.0	45
34.0	25	39.0	25
34.0	35	39.0	35
34.0	45	39.0	45
		39.8	25
		39.8	35
		39.8	45

*Ten postlarvae from each set of acclimation conditions was tested at each of the corresponding six sets of test conditions.

TABLE 9.--*Acclimation and test conditions used in the temperature-salinity experiment (low salinity range) on white shrimp**

Acclimation conditions		Test conditions	
Temperature	Salinity	Temperature	Salinity
29.0	5	38.5	5
29.0	15	28.5	15
29.0	25	38.5	25
		39.0	5
		39.0	15
		39.0	25
34.0	5	39.5	5
34.0	15	39.5	15
34.0	25	39.5	25
		40.0	5
		40.0	15
		40.0	25

*Ten postlarvae from each set of acclimation conditions were tested at each of the corresponding six sets of test conditions.

TABLE 10.--Acclimation and test conditions used in the temperature-salinity experiment (high salinity range) on white shrimp*

Acclimation conditions		Test conditions	
Temperature	Salinity	Temperature	Salinity
29.0	25	38.5	25
29.0	35	38.5	35
29.0	45	38.5	45
		39.0	25
		39.0	35
		39.0	45
34.0	25	39.5	25
34.0	35	39.5	35
34.0	45	39.5	45
		40.0	25
		40.0	35
		40.0	45

*Ten postlarvae from each set of acclimation conditions were tested at each of the corresponding six sets of test conditions.

Statistical Analysis

Statistical methods used are described in Snedecor and Cochran (1967) and Van Der Reyden (1943). All thermal resistance times were converted to logarithms for the statistical analyses. This is the common method of treating thermal resistance data, because conversion of the resistance times to logarithms gives a normal distribution of the data (Bigelow, 1921).

Factorial analysis was used to analyze the data from the thermal resistance and temperature-salinity experiments. In factorial analysis, the effects of the individual factors, and of the interactions between factors, are analyzed so as to determine if these factors and interactions significantly influence the variance of the resistance times.

In all statistical analyses, a probability of 0.05 or less was considered to be an indication that the factor in question had a significant effect on thermal resistance time. The probabilities were obtained from standard tables (Snedecor and Cochran, 1967).

If a significant value (0.05 or less) was found for a 3-way interaction ($A \times B \times C$) in the factorial analysis, each 2-way interaction was retested at each level of the third factor (i.e., $A \times B$ at each level of C ; $B \times C$ at each level of A , etc.). If a 2-way interaction was found to be significant, the effect of each factor was tested at every level of the other factor, using one-way analysis of variance.

Factorial analysis was used to determine interactions between time after transfer to the second acclimation temperature and species, magnitude of increase in acclimation temperature, and lethal temperature in the acclimation experiments. A significant interaction between the factor being tested (species, etc.) and time after transfer was considered to be an indication of different acclimation rates in the different levels of the factor being tested.

Each acclimation study was analyzed using the "orthogonal polynomials of least squares" method to determine the polynomial which best fit the data (Van Der Reyden, 1943). In this method, each term of the polynomial is tested to determine if it significantly reduces the unexplained variance. The term of highest degree which is found to be significant is considered to be the smallest degree of polynomial which will fit the data (Van Der Reyden, 1943).

This method requires that the X values be evenly spaced. Since the acclimation experiments consisted of tests at 1-day intervals for a certain period of time after which tests were conducted at 2-day intervals, the experiments were analyzed at both 1- and 2-day intervals. Thus, a particular acclimation experiment was fitted with a polynomial at 1-day intervals, beginning at 0 hours and covering the period over which tests at 1-day intervals were conducted. Then, the entire experiment was fitted with a polynomial using 2-day intervals, beginning at 0 hours and covering the entire experiment.

RESULTS

*Thermal Resistance Experiments**Brown Shrimp Postlarvae*

The individual resistance times of brown shrimp postlarvae from the thermal resistance experiment are shown in Figure 2. The two replications were combined (Fig. 2) because no significant differences between replications were found.

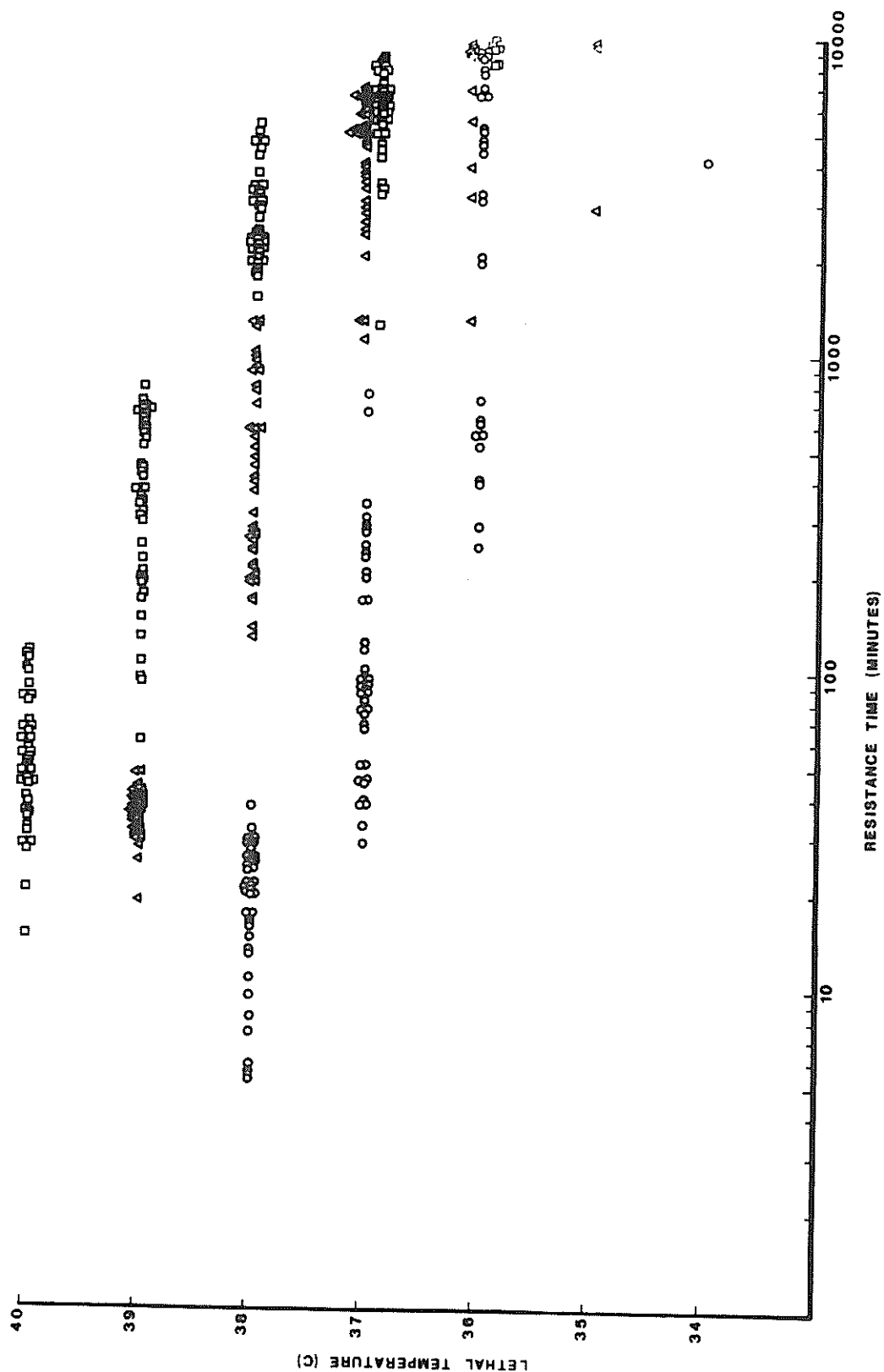
Over 50% of the postlarvae acclimated at 24 C and tested at 34 and 35 C survived for over 10,000 minutes (Fig. 2). Over 50% of those postlarvae acclimated at 29 C and tested at 35 and 36 C, and of those acclimated at 34 C and tested at 36 C, also survived for over 10,000 minutes (Fig. 2). At lethal temperatures of 37 C and above, all of the postlarvae acclimated at 24, 29 and 34 C died before 10,000 minutes (Fig. 2). Thus, the temperature which was lethal to 50% of the postlarvae at 10,000 minutes was between 35 and 36 C for postlarvae acclimated at 24 C, and between 36 and 37 C for postlarvae acclimated at 29 and 34 C.

While 36 C was not lethal at 10,000 minutes for most brown shrimp postlarvae acclimated at 29 and 34 C, some mortality at this temperature did occur (Fig. 2). This may indicate that 36 C would be lethal for postlarvae at times exceeding 10,000 minutes.

The 24-hour LC_{50} 's for each acclimation temperature may be determined by interpolation, if it is assumed that the relationship between

FIGURE 2.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 24 (O), 29 (Δ) and 34 (\square) C and tested at temperatures between 34 and 40 C. There were 40 postlarvae per test.

FIGURE 2



resistance time and lethal temperature is approximately linear. Using this method, the 24-hour LC_{50} 's for brown shrimp postlarvae were found to be: 36.3 C for postlarvae acclimated at 24 C, 37.5 C for postlarvae acclimated at 29 C, and 38.3 C for postlarvae acclimated at 34 C.

The median resistance times of brown shrimp postlarvae increased with increasing acclimation temperature at each lethal temperature (Fig. 3). This observation was supported by the statistical analysis, which found significant differences between acclimation temperatures; however, the difference between the median resistance time of postlarvae acclimated at 24 C and those acclimated at 29 C was greater than the difference between the median resistance time of postlarvae acclimated at 29 C and those acclimated at 34 C (Fig. 4).

The median resistance time also increased with decreasing lethal temperature at each of the three acclimation temperatures (Fig. 4). This is also indicated in the results of the statistical analysis; however, the rate of increase per 1 C decrease in lethal temperature varied between different lethal temperatures and at different acclimation temperatures (Fig. 4). Different effects of different levels of acclimation temperature and lethal temperature are also indicated by a significant interaction between these two factors. This indicates that resistance time at a given acclimation temperature-lethal temperature combination was not simply the result of the additive effects of acclimation and lethal temperature.

FIGURE 3.--Median thermal resistance times of brown shrimp postlarvae acclimated at 24, 29, and 34 C and tested at 37 (●), 38 (△), and 39 (□) C.

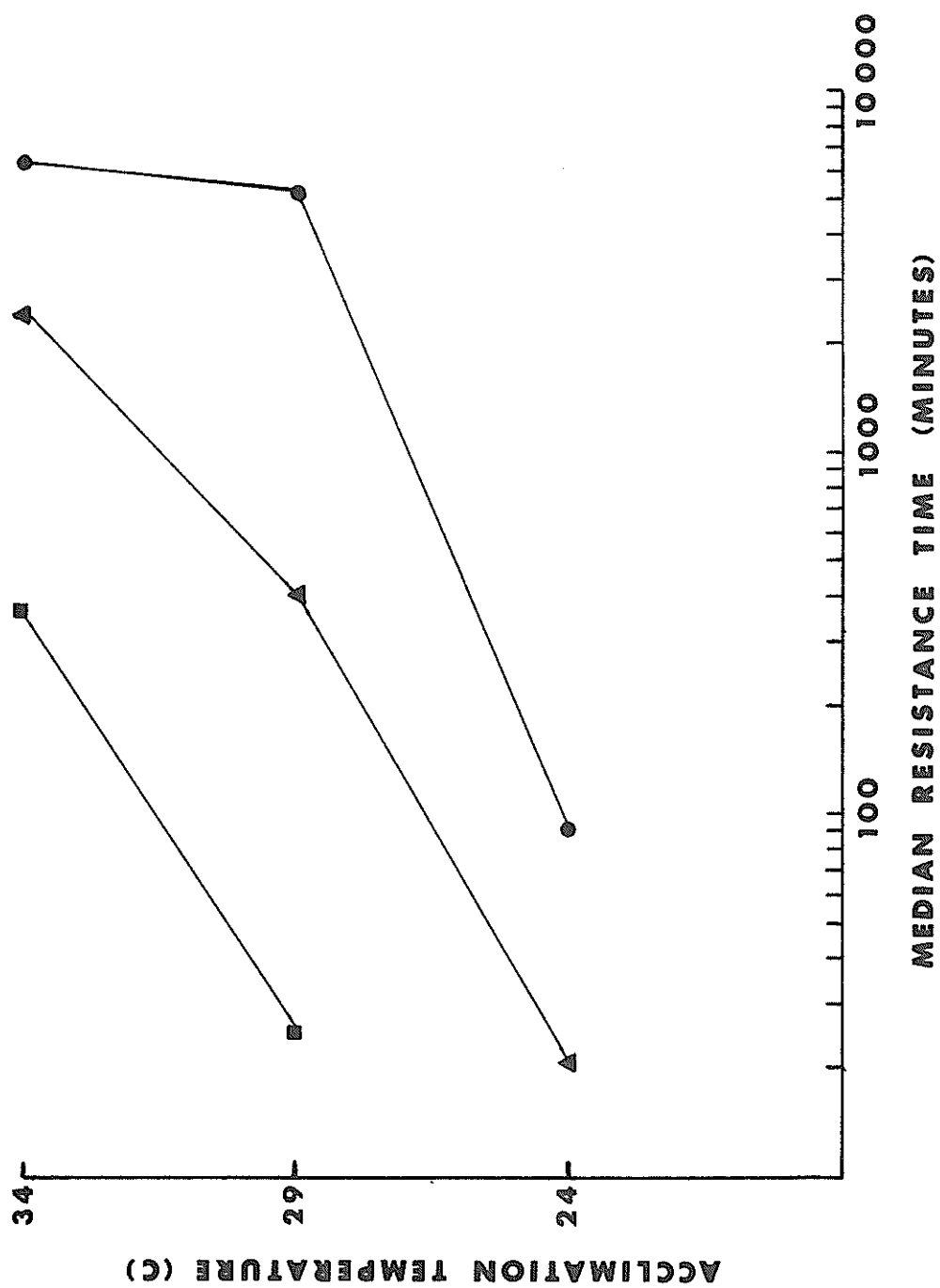
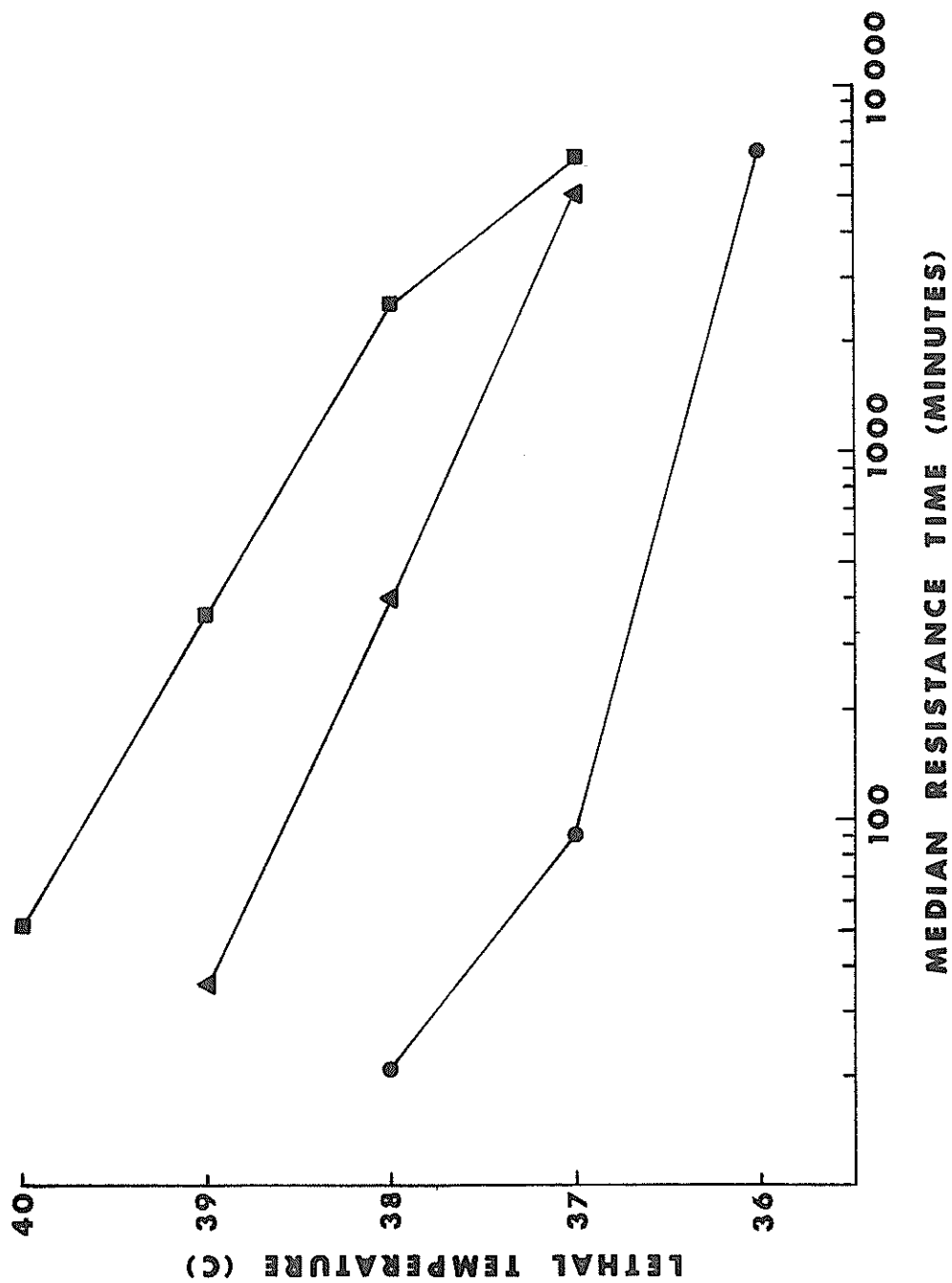


FIGURE 4.--Median thermal resistance times of brown shrimp postlarvae at lethal temperatures of 36, 37, 38, 39, and 40 C after acclimation at 24 (O), 29 (Δ), and 34 (\square) C.



Brown Shrimp - 30 mm

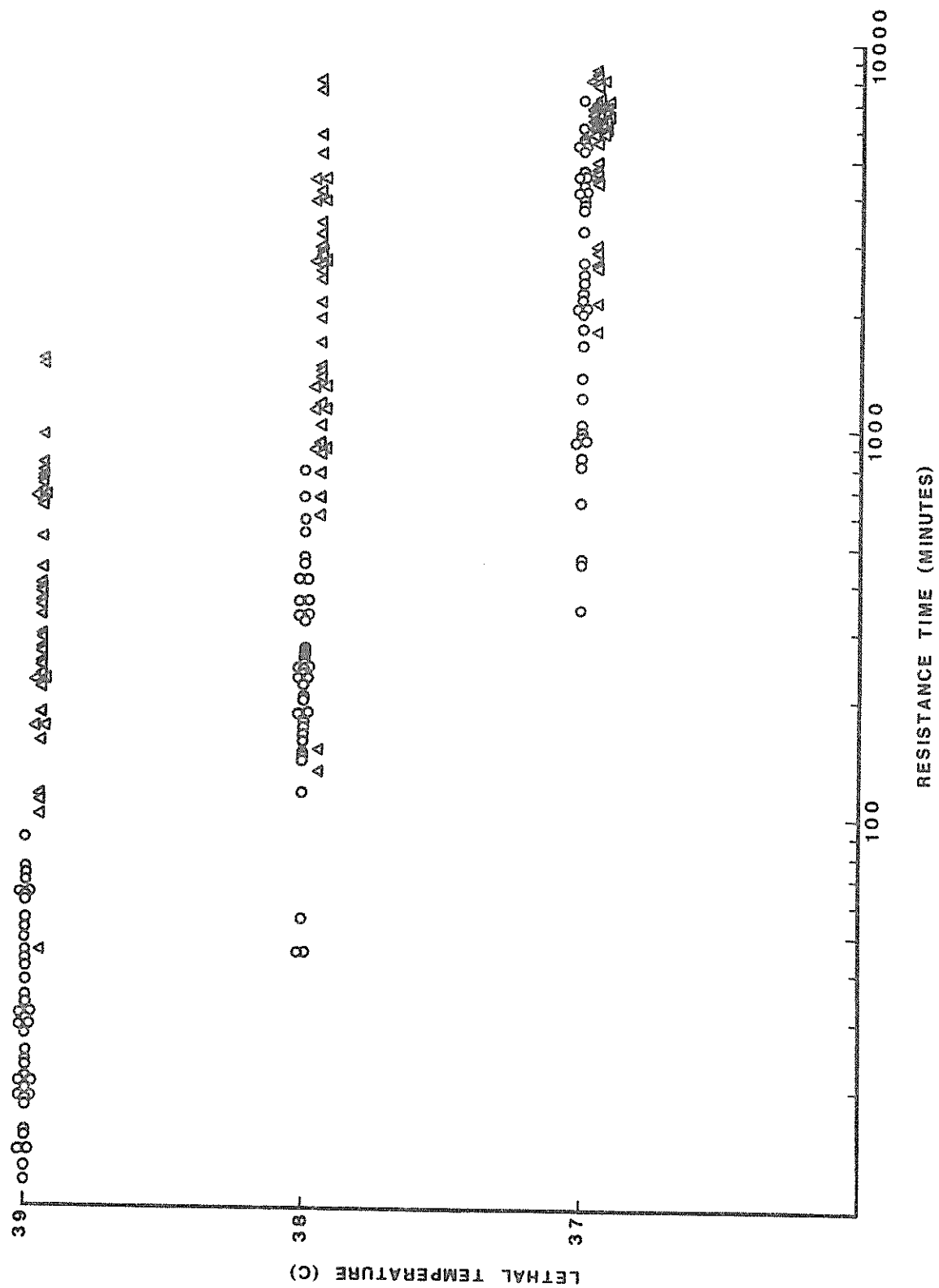
The individual resistance times of 30 mm brown shrimp from the thermal resistance experiment are given in Figure 5. The two replications were combined, as there were no significant differences between replications. All of the shrimp tested in this experiment died before 10,000 minutes (Fig. 5).

Factorial analyses comparing the postlarval and 30 mm brown shrimp in thermal resistance experiments indicates there were significant differences between the two age groups at lethal temperatures of 37 and 38 C for shrimp acclimated at 29 C, and at 38 C for shrimp acclimated at 34 C. There was no significant difference in thermal resistance between postlarvae and 30 mm brown shrimp at a lethal temperature of 39 C for shrimp acclimated at 29 and 34 C, or at a lethal temperature of 37 C for shrimp acclimated at 34 C.

It may be that the shrimp tested at 39 C were affected by the temperature so quickly that possible differences due to size group did not become apparent. A reduction of the differences in thermal resistance due to salinity effects at rapidly lethal temperatures would seem to suggest this (see below). At a lethal temperature of 37 C, a strong lethal effect at close to 10,000 minutes may have hidden differences between brown and white shrimp acclimated at 34 C (see below). This may also explain the absence of a significant difference in thermal resistance between 30 mm and postlarval brown shrimp at a

FIGURE 5.--Individual thermal resistance times of 30 mm brown shrimp acclimated at 29 (O) and 34 (Δ) C and tested at 37, 38, and 39 C. There were 40 shrimp per test.

FIGURE 5



lethal temperature of 37 C.

The effect of age group on thermal resistance in brown shrimp is somewhat ambiguous, and differences should be interpreted cautiously. However, significant interactions between age group and lethal temperature, and between age group and acclimation temperature, indicate that the two groups responded differently to different acclimation and lethal temperatures. This may also be an indication of real differences between the two age groups.

The median thermal resistance time increased with increasing acclimation temperature at each of the three lethal temperatures (Fig. 6). The median resistance time also increased with decreasing lethal temperature at both acclimation temperatures (Fig. 7). All of these differences were statistically significant.

The differences between the median resistance times of shrimp acclimated at 29 C and of those acclimated at 34 C was less at a lethal temperature of 37 C than at lethal temperatures of 38 or 39 C, indicating differences in the effects of acclimation and lethal temperatures on resistance time (Fig. 7), which is also suggested by the statistically significant interaction of acclimation and lethal temperatures.

White Shrimp Postlarvae

The individual resistance times of the white shrimp postlarvae from this experiment are shown in Figure 8. There was no significant difference between replications, so they were combined.

FIGURE 6.--Median thermal resistance times of 30 mm brown shrimp acclimated at 29 and 34 C and tested at 37 (O), 38 (Δ), and 39 (\square) C.

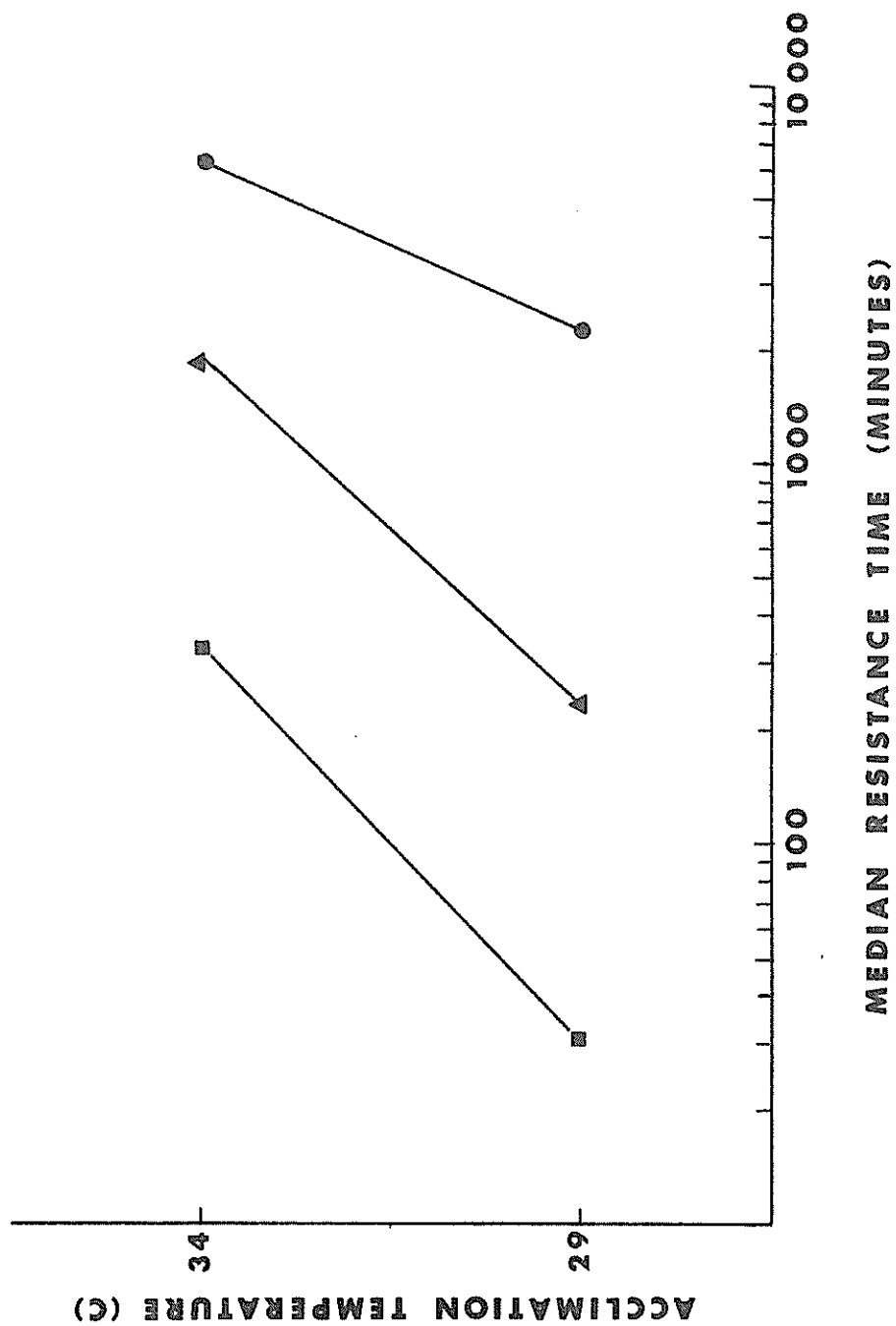
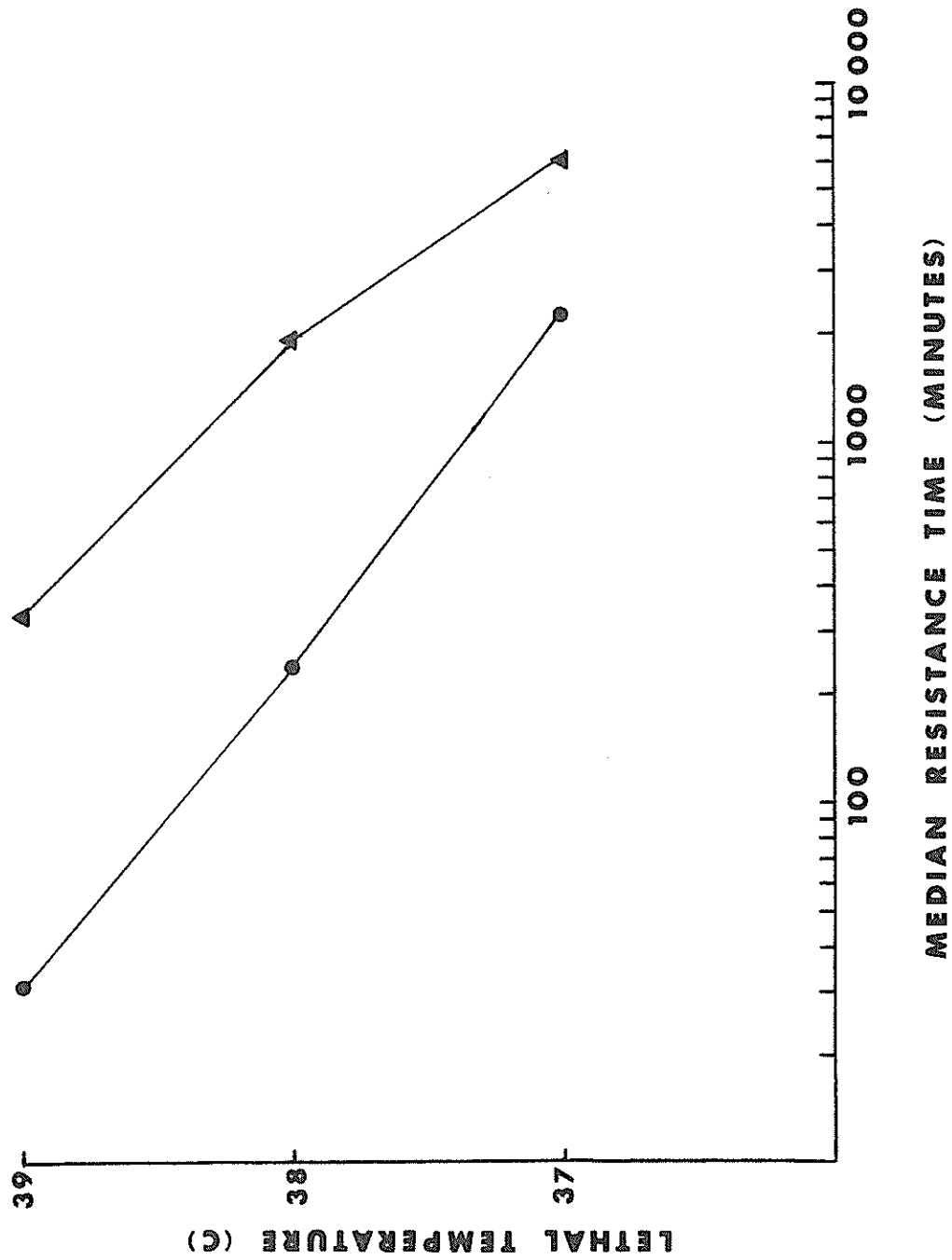


FIGURE 7.--Median thermal resistance times of 30 mm brown shrimp at lethal temperatures of 37, 38, and 39 C after acclimation at 29 (O) and 34 (Δ) C.



Over 50% of the postlarvae acclimated at 29 C and tested at 35 and 36 C survived for over 10,000 minutes (Fig. 8). Over 50% of the postlarvae acclimated at 34 C and tested at 36 C also survived for over 10,000 minutes (Fig. 8). At lethal temperatures of 37 C and higher, at least 50% of the postlarvae died before 10,000 minutes (Fig. 8). Thus, the temperature which was lethal to 50% of the postlarvae at 10,000 minutes was between 36 and 37 C for shrimp acclimated at 29 and 34 c. The 24-hour LC_{50} 's for white shrimp postlarvae, which were also determined by interpolation, were found to be: 38.3 C for postlarvae acclimated at 29 C, and 38.9 C for postlarvae acclimated at 34 C.

The median resistance time of white shrimp postlarvae increased with increasing acclimation temperature at all lethal temperatures except 37 C (Fig. 9). The median resistance time also increased with decreasing lethal temperature (Fig. 10). There were statistically significant differences between different acclimation temperatures within all lethal temperatures except 37 C, and between different lethal temperatures within all acclimation temperatures.

Species Comparison

The individual resistance times of brown shrimp postlarvae which were collected at the same time and acclimated and tested under the same conditions as the white shrimp postlarvae are shown in Figure

FIGURE 8.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 (O) and 34 (Δ) C and tested at temperatures between 36 and 41 C. There were 40 shrimp per test.

FIGURE 8

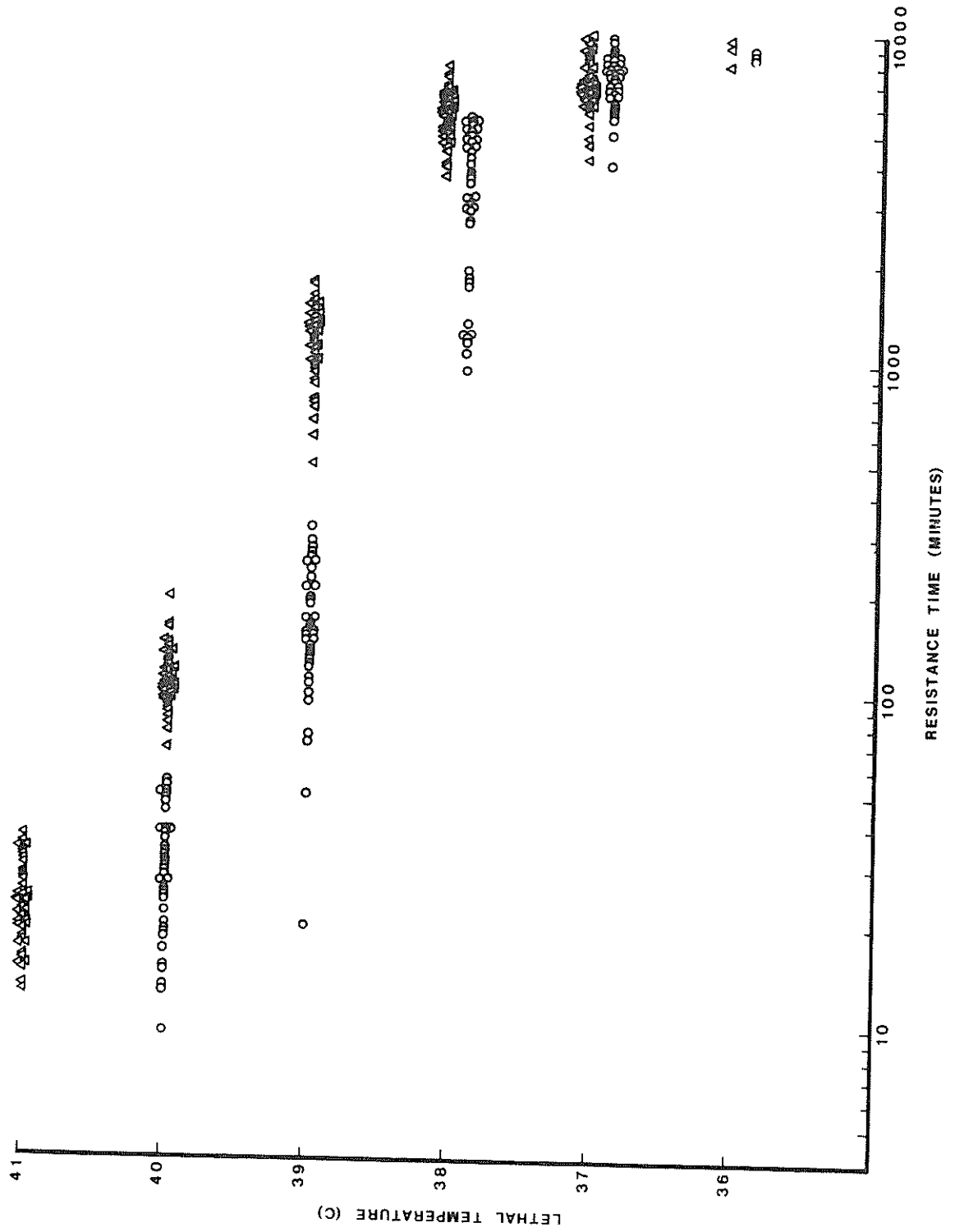


FIGURE 9.--Median thermal resistance times of white shrimp postlarvae acclimated at 29 and 34 C and tested at 37 (●), 38 (△), 39 (□), and 40 (○) C.

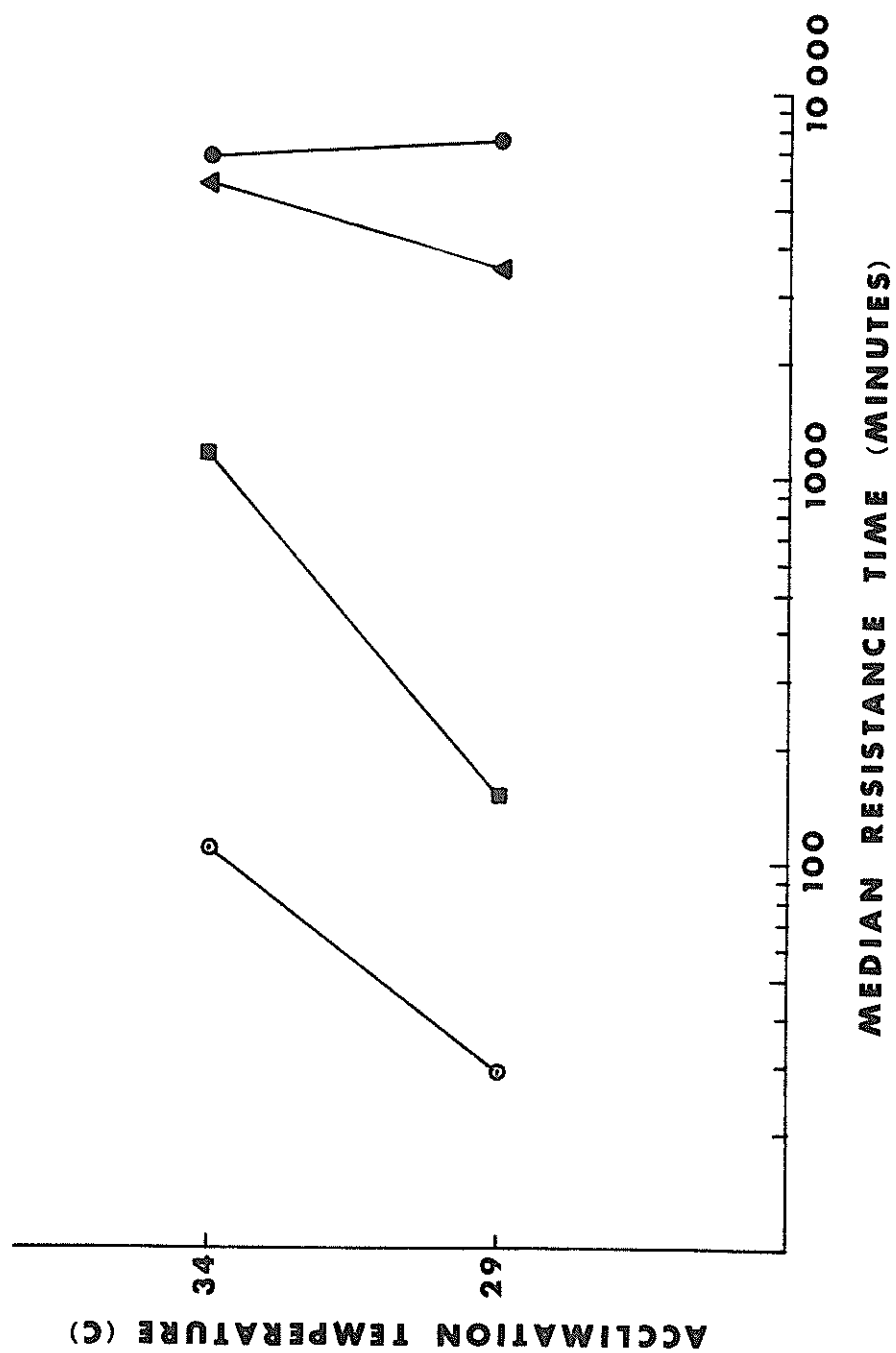
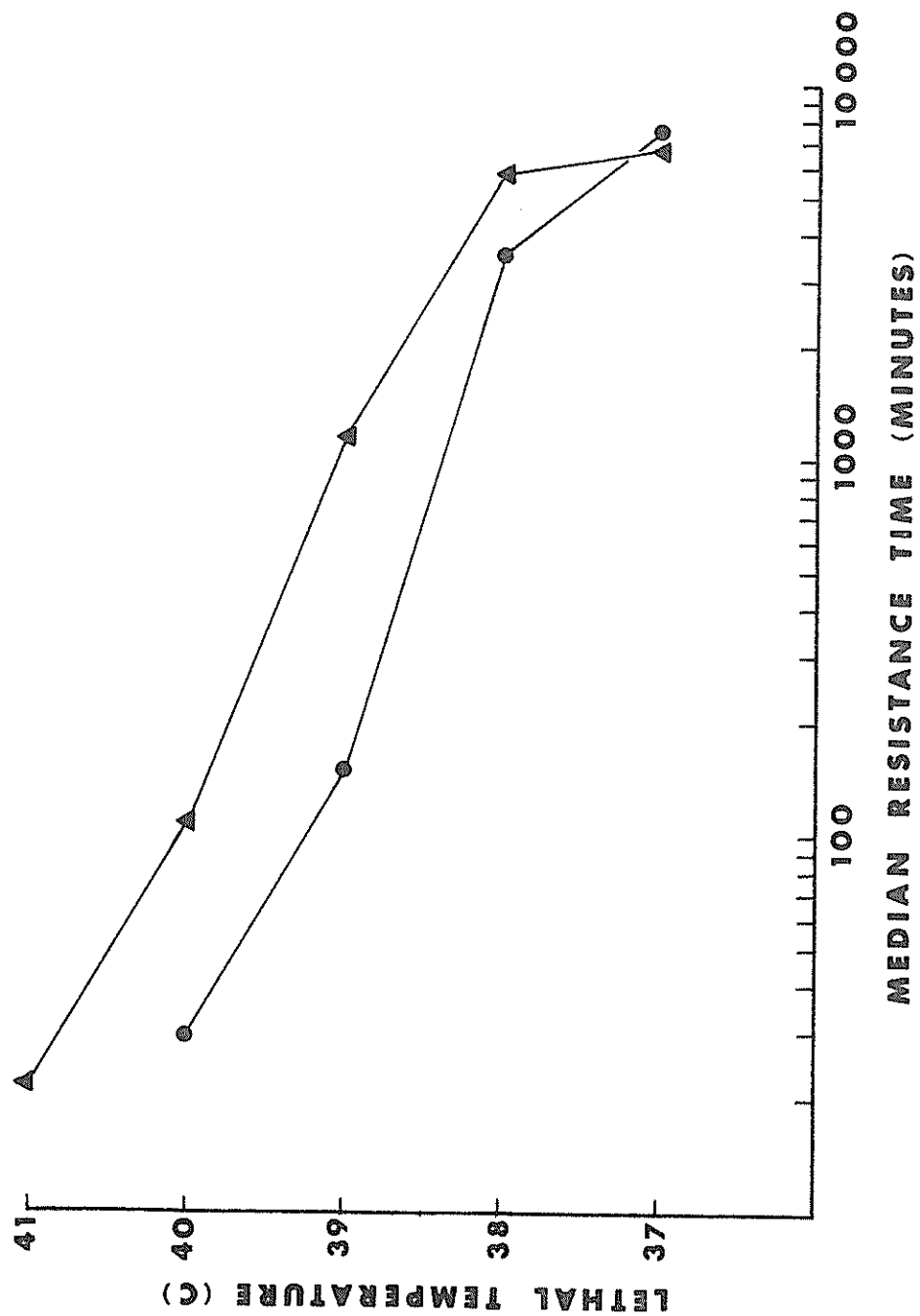


FIGURE 10.--Median thermal resistance times of white shrimp postlarvae at lethal temperatures of 37, 38, 39, 40, and 41 C after acclimation of 29 (O) and 34 (Δ) C.



11. There were no significant differences between replications, so they were combined. All of the postlarvae died before 10,000 minutes at the temperatures at which they were tested (37-40 C) (Fig. 11).

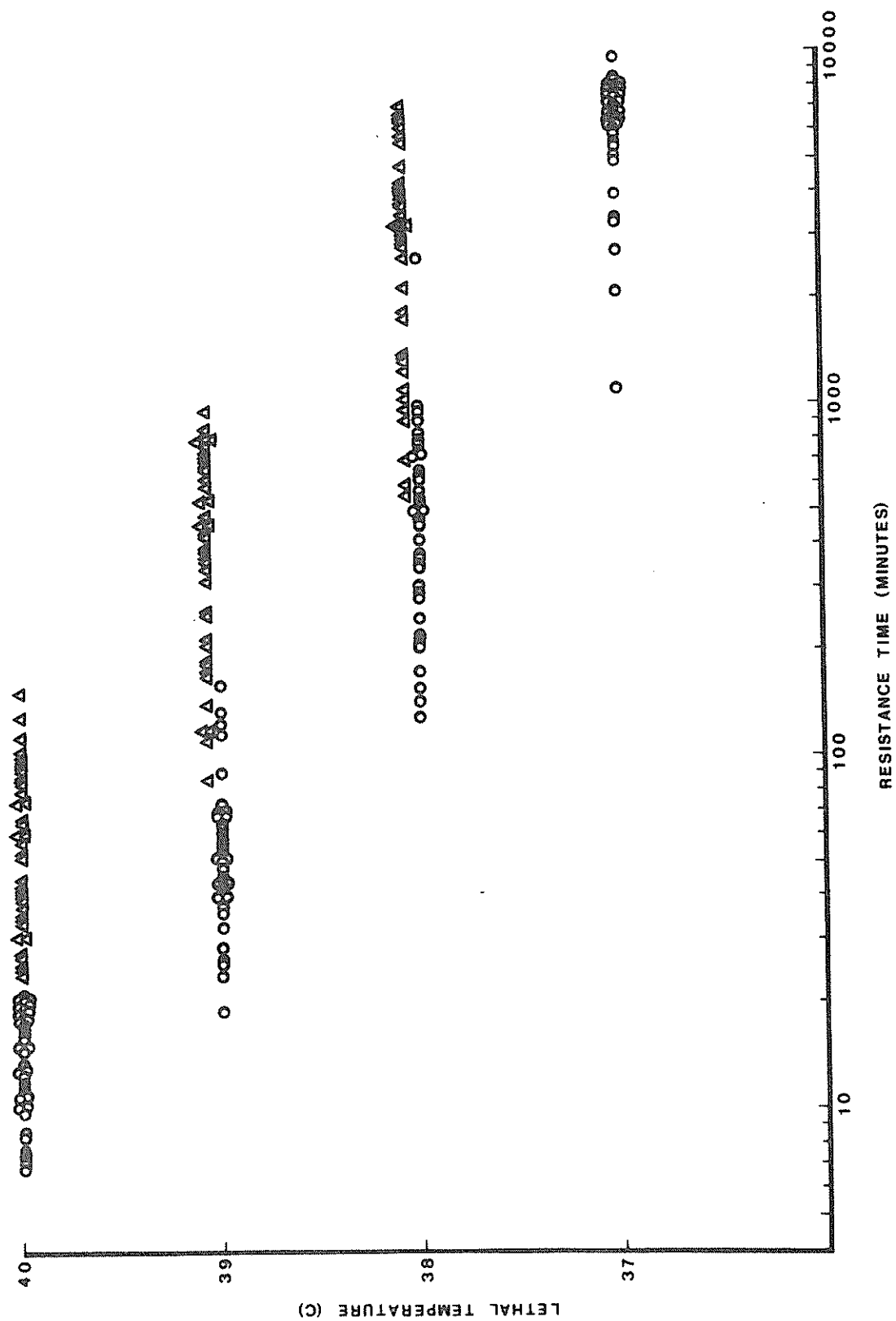
A direct comparison of thermal resistance of these brown shrimp postlarvae and the white shrimp postlarvae collected at the same time indicated that there were significant differences between the two species. The white shrimp postlarvae were somewhat more resistant than the brown shrimp postlarvae. This was true at all of the acclimation temperature-lethal temperature combinations at which they were compared, and these differences were statistically significant.

There was a significant two-way interaction between species and acclimation temperatures at a lethal temperature of 38 C, but not at 39 or 40 C. This indicated that the effects of acclimation temperature on thermal resistance were generally similar in both species, at least at the higher lethal temperatures.

The two-way interactions of lethal temperature and species were significant at both acclimation temperatures. This would seem to indicate that each species reacted differently to a given lethal temperature. Thus, the difference in thermal resistance between the two species seems to be mainly due to a greater ability of white shrimp to resist the effects of the lethal temperatures, rather than to a difference in the effects of acclimation temperature between the two species.

FIGURE 11.--Individual thermal resistance times of brown shrimp postlarvae collected at the same time as the white shrimp postlarvae (September), acclimated at 29 (O) and 34 (Δ) C, and tested at temperatures between 37 and 40 C. There were 40 postlarvae per test.

FIGURE 11



The median resistance times of these postlarvae increased with increasing acclimation temperature (Fig. 12), and increased with decreasing lethal temperatures (Fig. 13). These differences were statistically significant.

Seasonal Effects

Factorial analysis was used to compare the thermal resistance of the brown shrimp postlarvae collected at the same time as the white shrimp postlarvae (September) with the thermal resistance of the brown shrimp postlarvae collected and tested earlier in the year (April). The results of this comparison indicated that there was little seasonal effect on thermal resistance in this species. Analysis of variance of the effect of season at each of the acclimation and lethal temperatures indicated that there was only one significant difference between seasons, at 29 C acclimation temperature and 39 C lethal temperature.

White Shrimp - 30 and 50 mm

The individual resistance times for the thermal resistance experiment on 30 mm white shrimp are shown in Figure 14, and those for 50 mm shrimp in Figure 15. There were no significant differences between replications, so they were combined.

The median resistance time for both 30 and 50 mm white shrimp generally increased with increasing acclimation temperature, but not at the same rate at different lethal temperatures (Fig. 16 and 17).

FIGURE 12.--Median thermal resistance times of brown shrimp postlarvae collected at the same time as the white shrimp postlarvae, acclimated at 29 and 34 C, and tested at 38 (O), 39 (Δ), and 40 (\square) C.

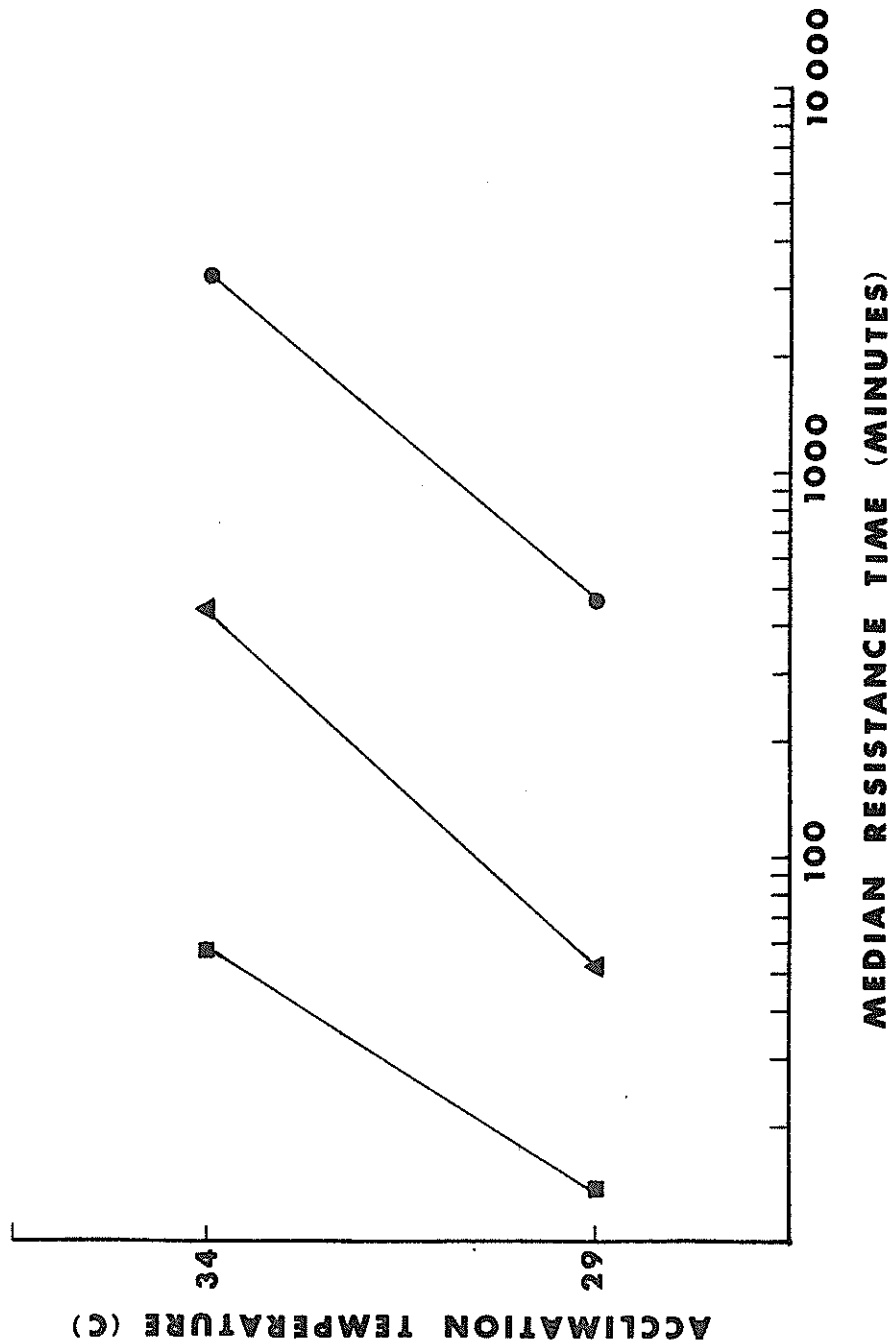


FIGURE 13.--Median thermal resistance times of brown shrimp postlarvae collected at the same time as the white shrimp postlarvae at lethal temperatures of 37, 38, 39, and 40 C after acclimation at 29 (O) and 34 (Δ) C.

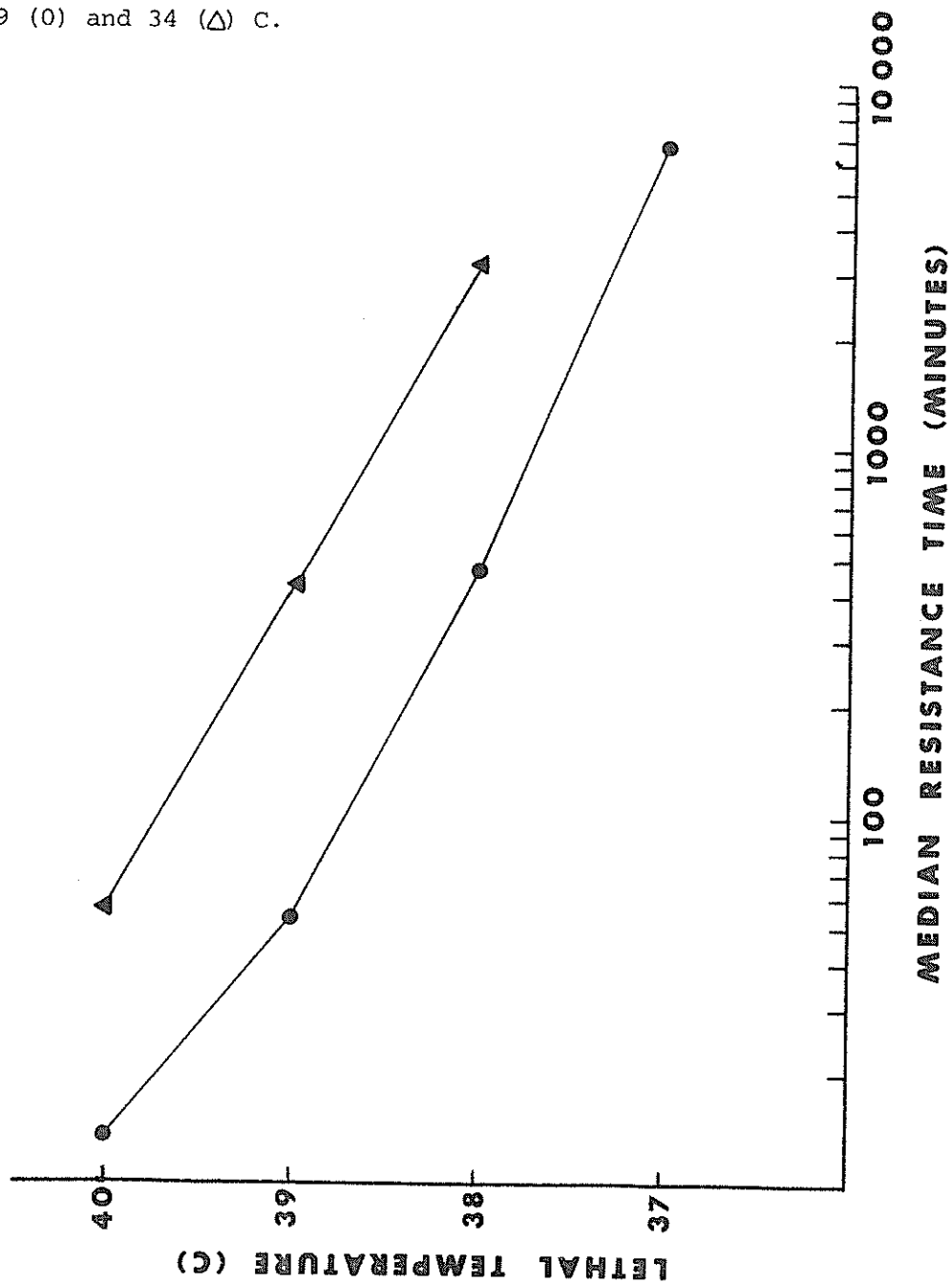


FIGURE 14.--Individual thermal resistance times of 30 mm white shrimp acclimated at 24 (O), 29 (Δ), and 34 (\square) C and tested at temperatures between 34 and 40 C. There were 20 shrimp per test.

FIGURE 14

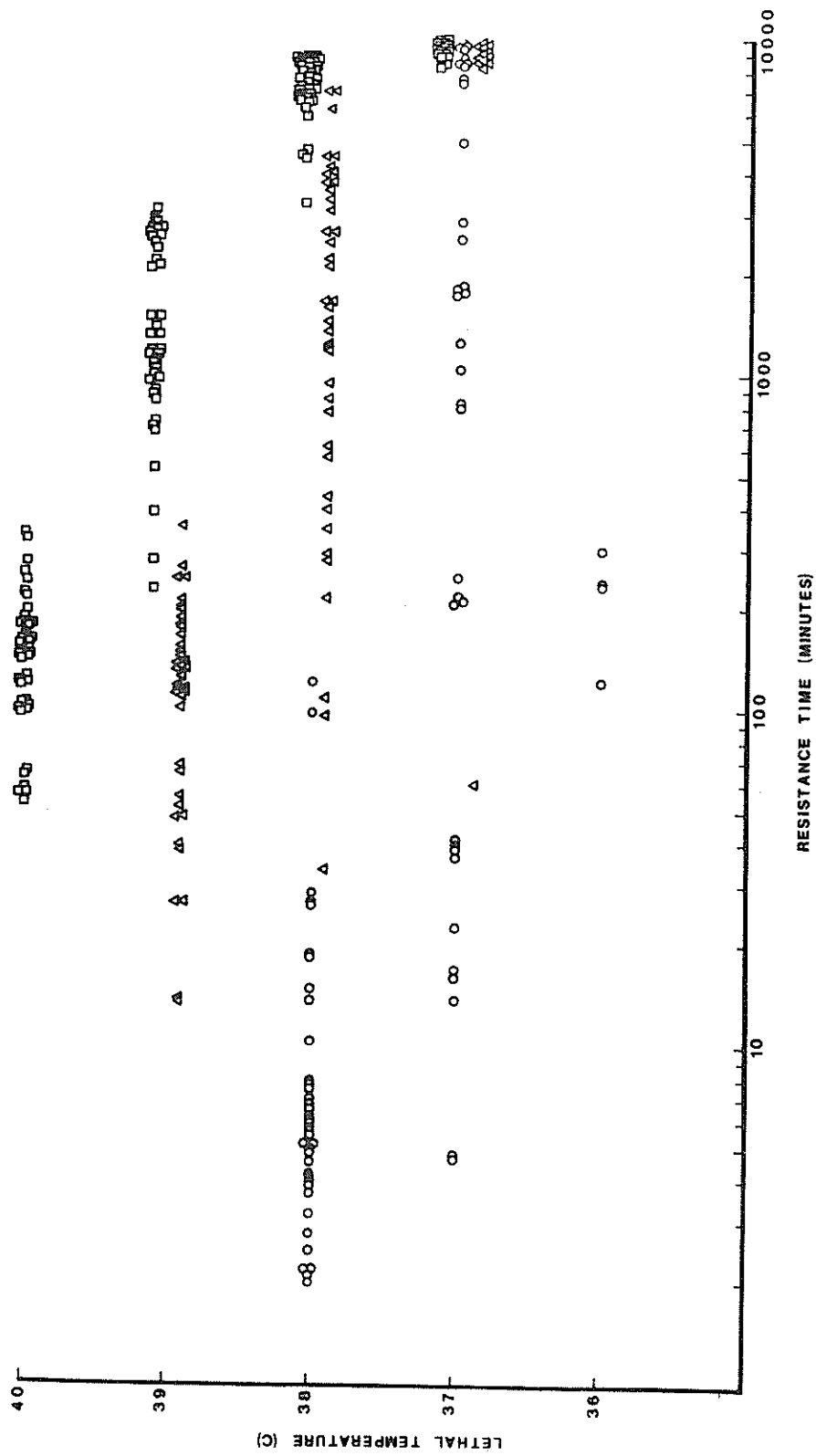


FIGURE 15.--Individual thermal resistance times of 50 mm white shrimp acclimated at 24 (O), 29 (Δ), and 34 (\square) C and tested at temperatures between 36 and 40 C. There were 20 postlarvae per test.

FIGURE 15

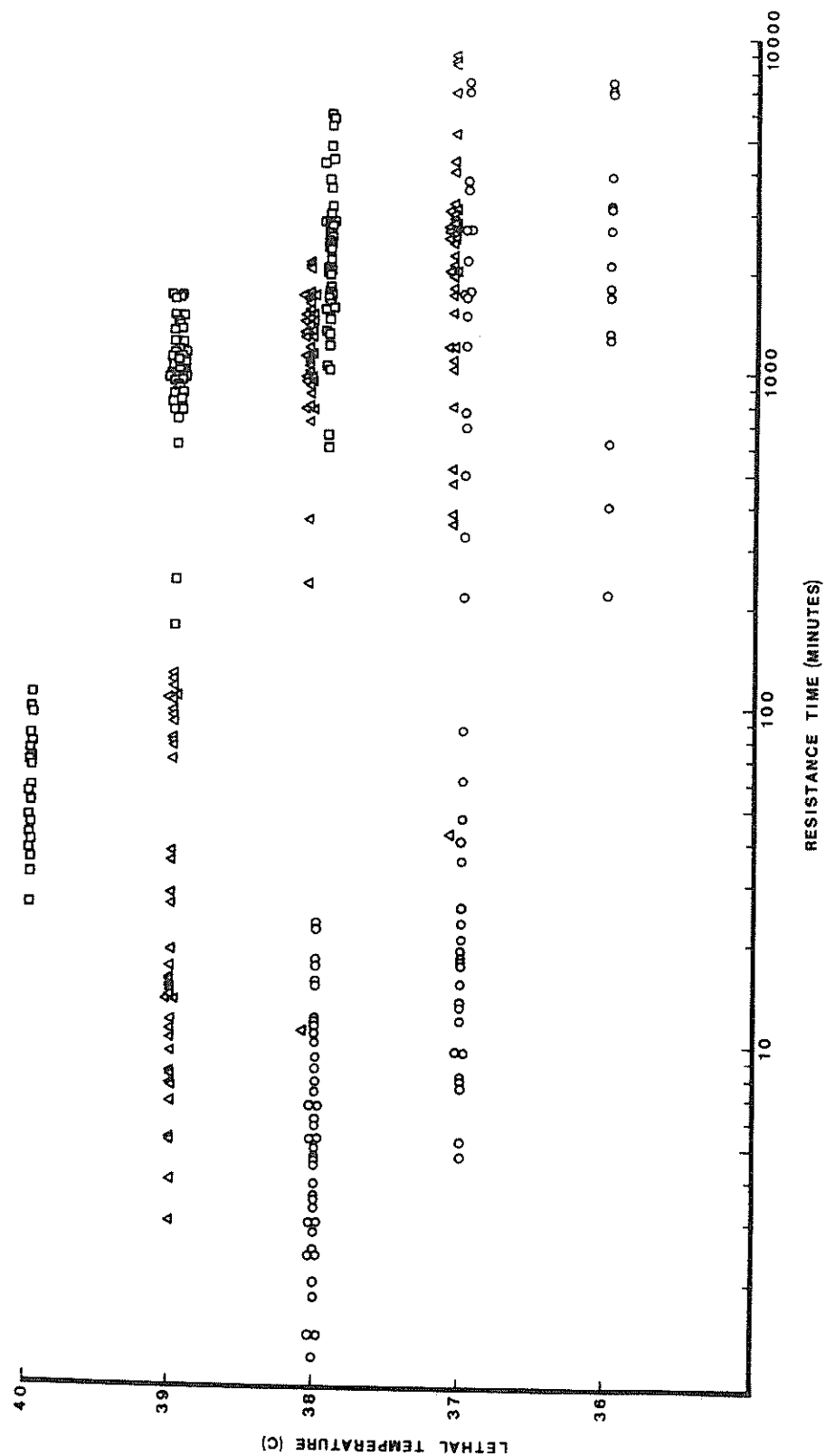


FIGURE 16.--Median thermal resistance times of 30 mm white shrimp at 37 (O), 38 (Δ), and 39 (\square) C after acclimation at 24, 29, and 34 C.

FIGURE 16

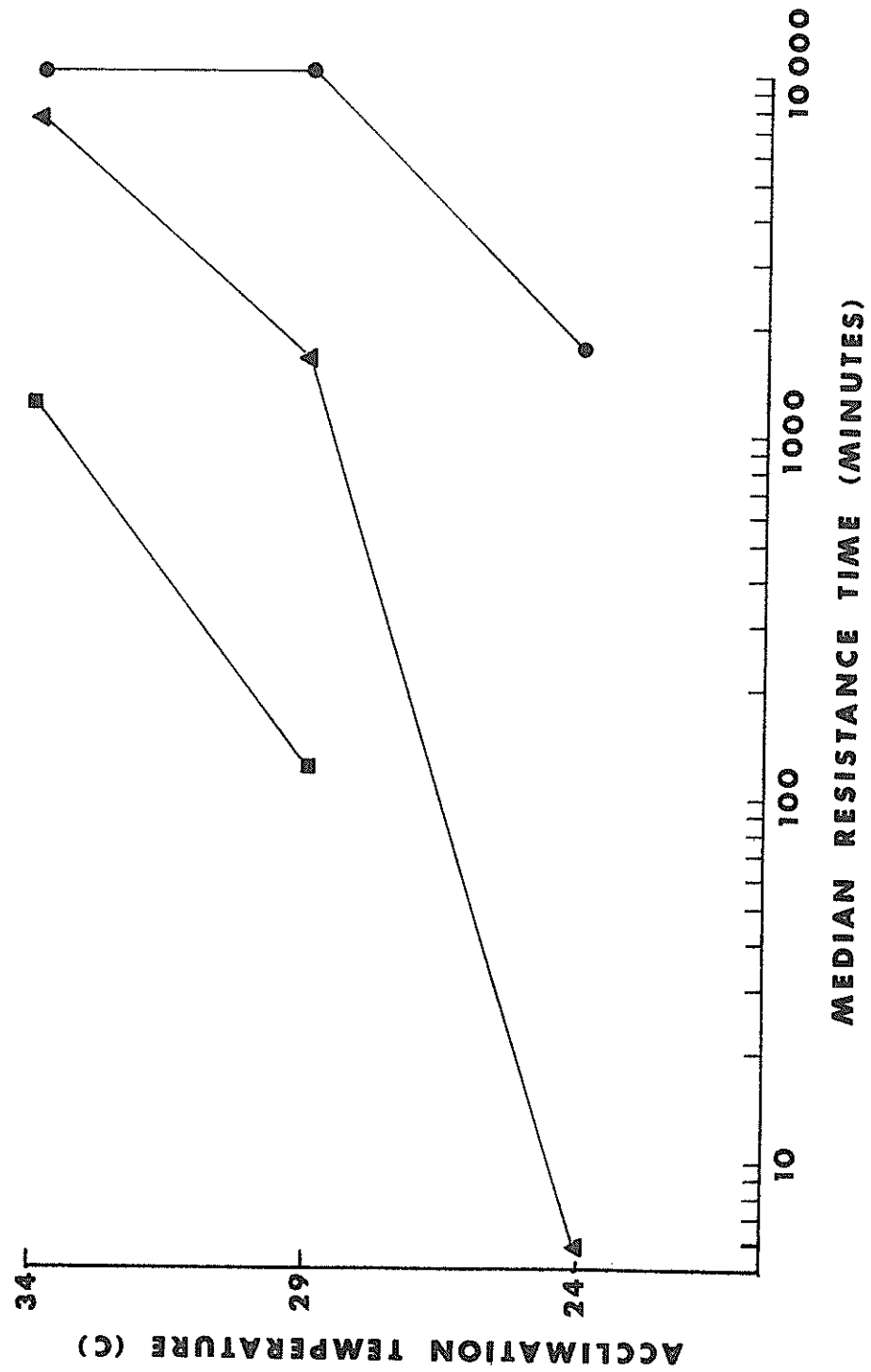
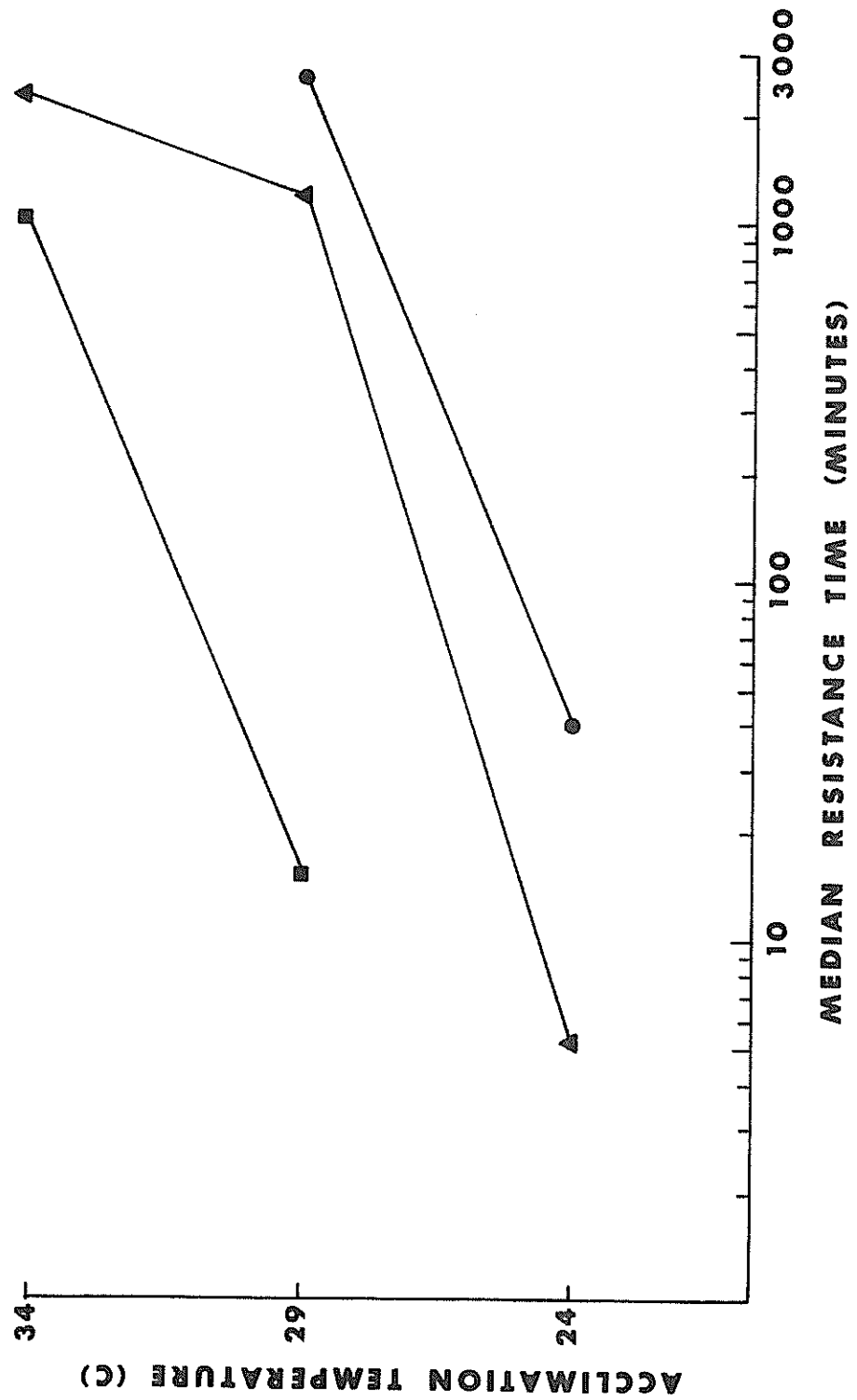


FIGURE 17.--Median thermal resistance times of 50 mm white shrimp at 37 (O), 38 (Δ), and 39 (\square) C after acclimation at 24, 29, and 34 C.

FIGURE 17



The median resistance time for both 30 and 50 mm white shrimp generally increased with increasing acclimation temperature, but not at the same rate at different lethal temperatures (Fig. 16 and 17).

The median resistance time increased with decreasing lethal temperature, but the amount of increase between lethal temperatures varied between different acclimation temperatures (Fig. 18 and 19). Analysis of variance indicated that the differences due to different levels of acclimation temperature were significant at all levels of lethal temperature and that the differences in lethal temperature were significant at all levels of acclimation temperature.

A comparison of the postlarvae, 30 mm, and 50 mm white shrimp thermal resistance times indicated significant differences between the different age groups at all acclimation temperature-lethal temperature combinations. Inspection of the data, however, indicated that the main difference was between 50 mm shrimp and the other two age groups, with postlarvae and 30 mm shrimp having similar resistance times. In fact, the 30 mm shrimp were more resistant than the postlarvae at certain acclimation temperature-lethal temperature combinations (Fig. 8 and 15). This would seem to indicate that white shrimp undergo a reduction in thermal resistance only after reaching 30 mm, while brown shrimp undergo this reduction before reaching 30 mm (see above). However, there may be other reasons for the similarity in thermal resistance in postlarval and 30 mm white shrimp. The two groups were from different sources, the postlarvae were "wild" and the 30 mm shrimp hatchery-reared, thus, the

FIGURE 18.--Median thermal resistance times of 30 mm white shrimp acclimated at 24 (O), 29 (Δ), and 34 (\square) C and tested at 37, 38, 39, and 40 C.

FIGURE 18

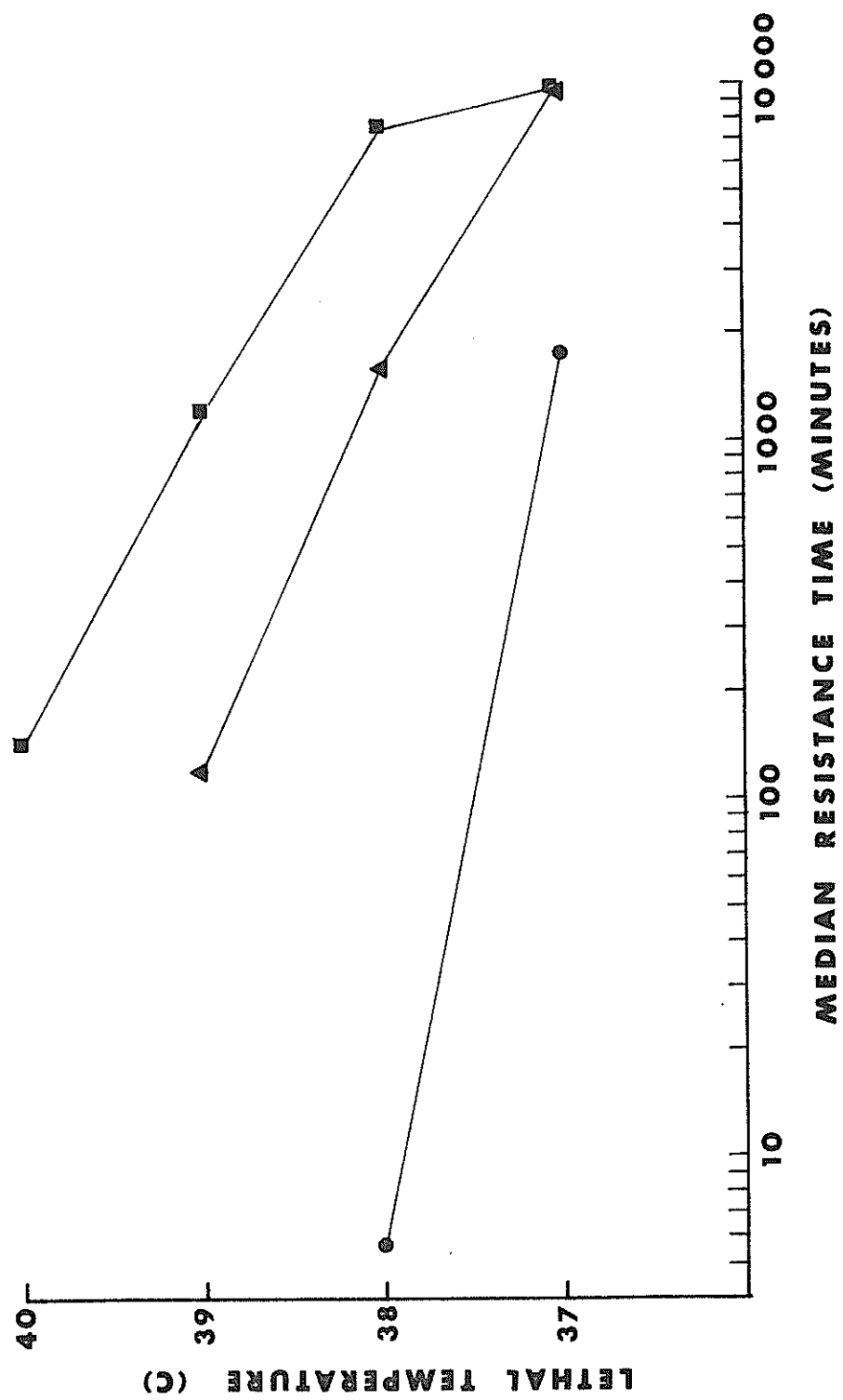
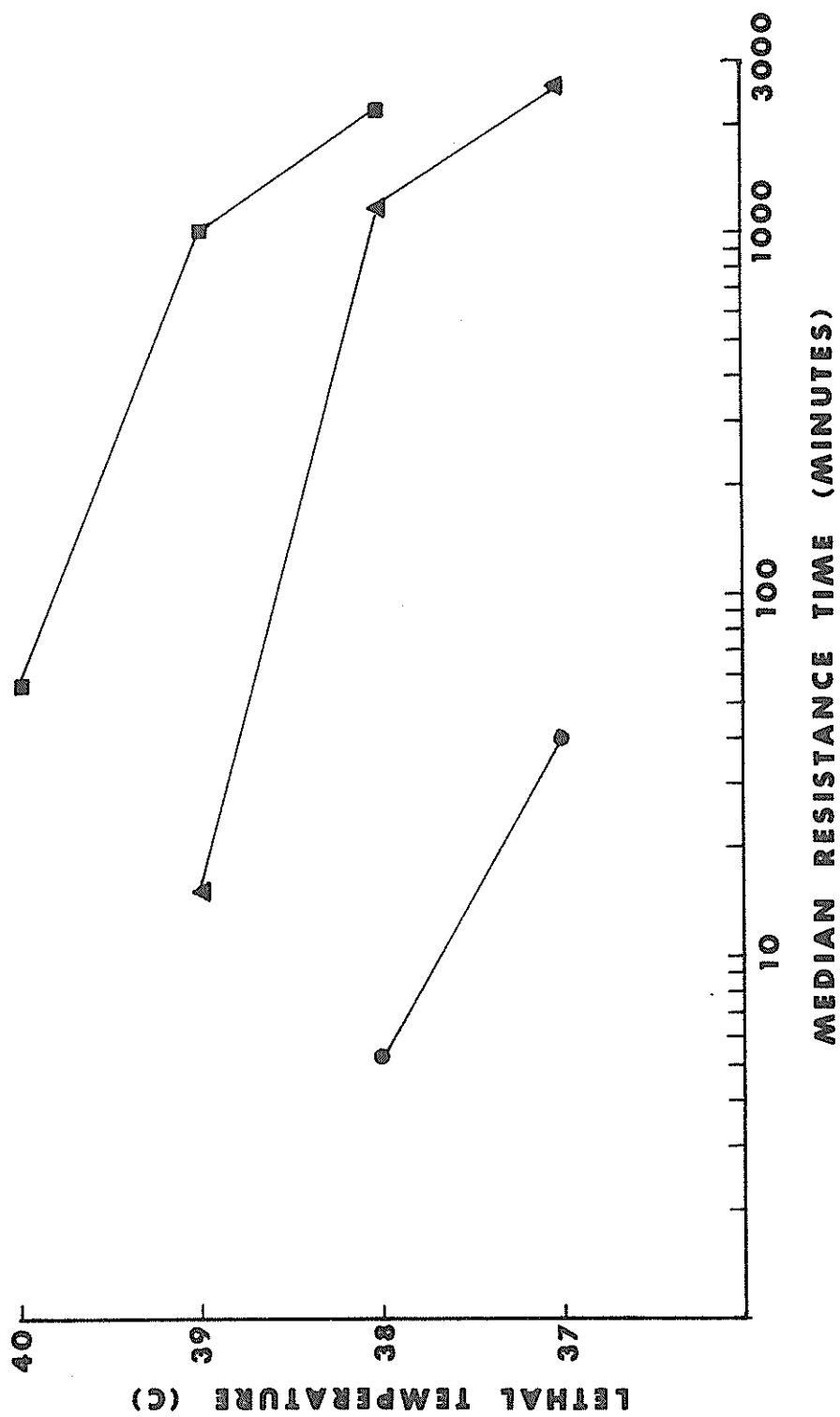


FIGURE 19.--Median thermal resistance times of 50 mm white shrimp acclimated at 24 (O), 29 (Δ), and 34 (\square) C and tested at 37, 38, 39, and 40 C.

FIGURE 19



similarity in thermal resistance in the two groups may have been due to genetic or selective factors which caused the 30 mm group to be more resistant. However, a recent comparison of resistance to cold shock (Sammy M. Ray, personal communication) found that wild brown shrimp postlarvae were more resistant than hatchery-reared postlarvae.

Significant interactions between age groups and lethal temperature and between age groups and acclimation temperature were also present. These interactions also seem to suggest differences between age groups in white shrimp.

Within major size groups (postlarvae, 30 mm and 50 mm), different size factors, such as length, weight, or K factor did not have any correlation with thermal resistance. Therefore, the differences between age groups are probably not due to differences in size *per se*.

Acclimation Experiments

Brown Shrimp Postlarvae

The individual resistance times of brown shrimp postlarvae which were subjected to increases in acclimation temperature are shown in Figures 20, 21, and 22. The two replications are combined in these figures because no significant differences between replications were found.

FIGURE 20.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 25 C, transferred to 30 C, and tested at 38.7 C. Tests were conducted at: just before transfer; 3, 12 and 24 hours after transfer; 1-day intervals from 1 to 16 days; and 2-day intervals from 16 to 22 days. There were 20 postlarvae per test.

FIGURE 20

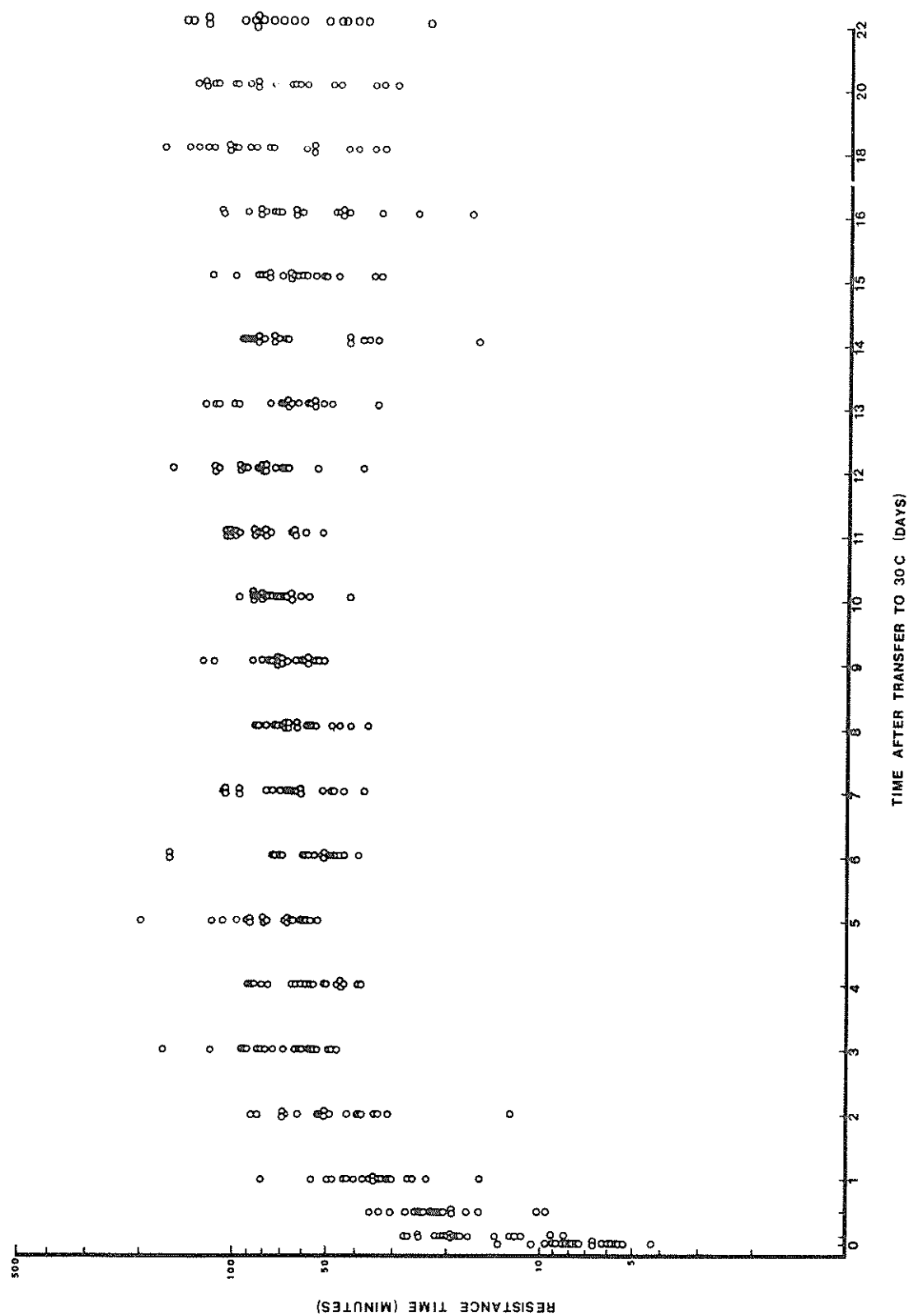


FIGURE 21.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 25 C, transferred to 30 C, and tested at 38.3 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 10 days; and 2-day intervals from 10 to 14 days. There were 20 postlarvae per test.

FIGURE 21

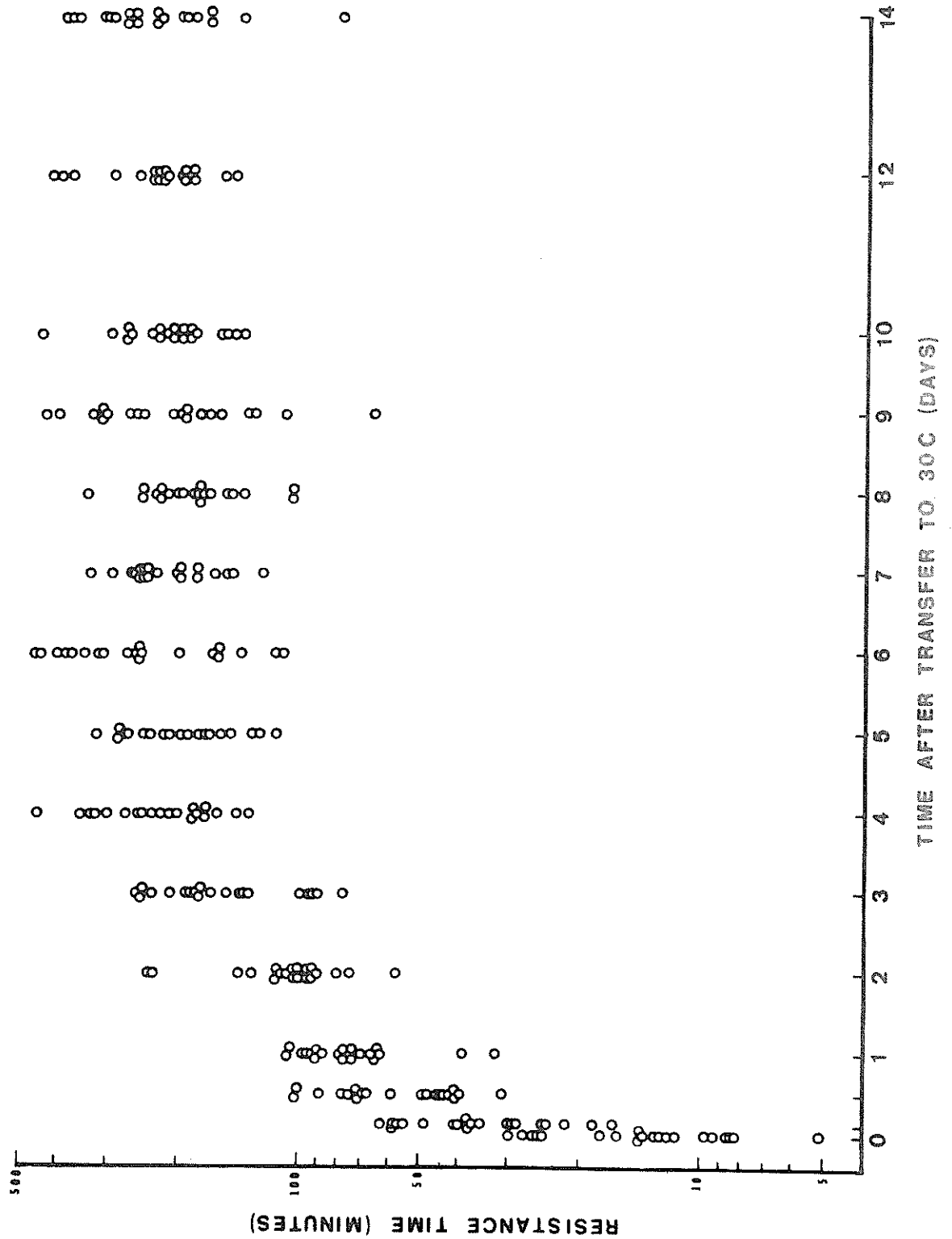
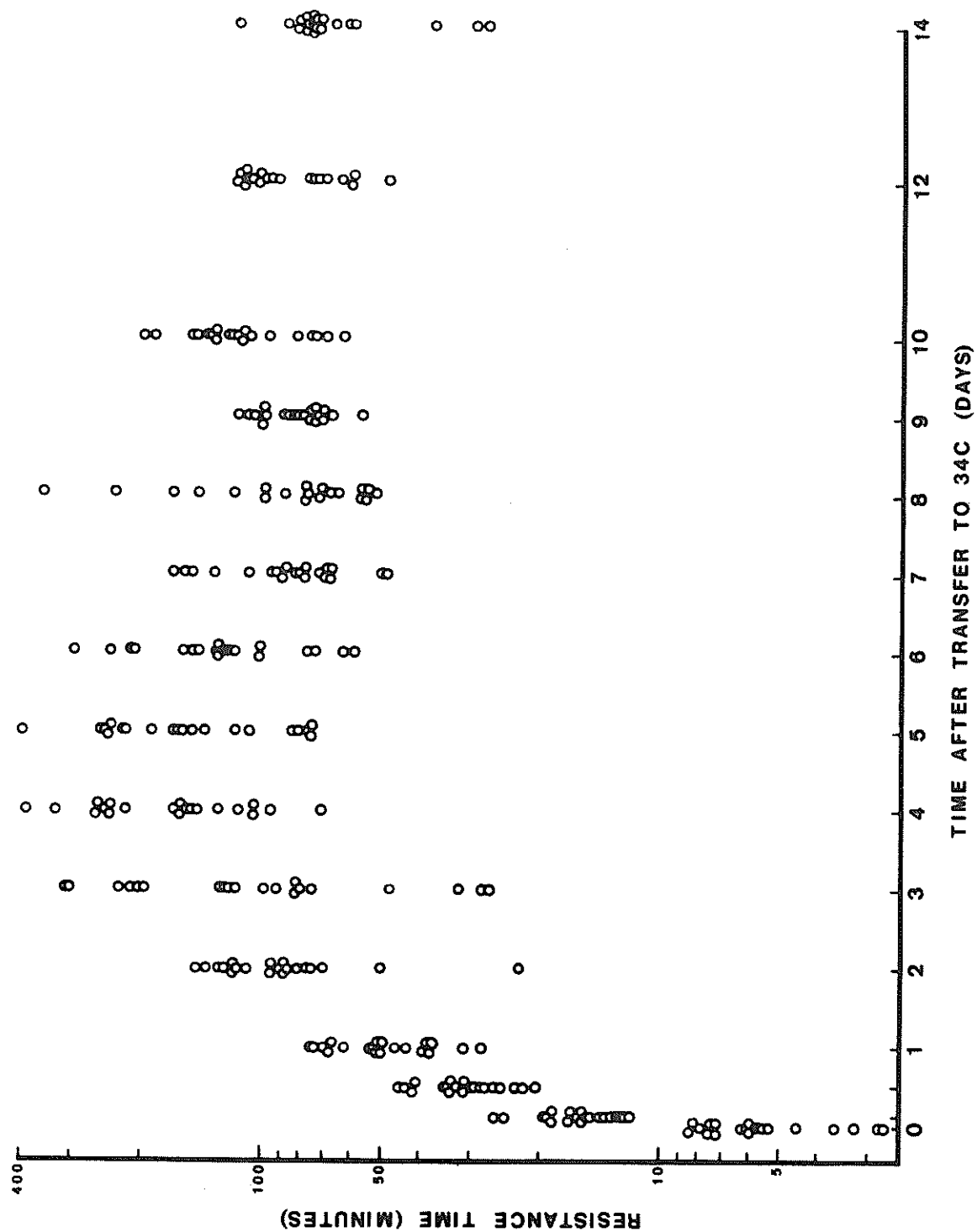


FIGURE 22.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 25 C, transferred to 34 C, and tested at 39.5 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 10 days after transfer; and 2-day intervals from 10 to 14 days after transfer. There were 20 postlarvae per test.

FIGURE 22



Brown shrimp postlarvae seemed to complete most of their acclimation to an increase in temperature in 3-4 days. Differences in lethal temperature did not affect the rate of acclimation to a 5 C increase in acclimation temperature (Fig. 20 and 21). Statistical analyses of these two experiments found no interaction between lethal temperature and time after transfer. Since lack of interaction indicates that lines fitted to the means of the individual tests in each of the experiments are essentially parallel, it appears that the rate of acclimation is the same in both experiments.

While the initial period of acclimation was the same in brown shrimp postlarvae subjected to a 5 C and a 9 C increase in acclimation temperature, there were differences in the pattern of acclimation. Postlarvae undergoing a 9 C increase in acclimation temperature apparently overshoot the level of thermal resistance consistent with the higher (34 C) acclimation temperature (Fig. 22).

In both experiments in which brown shrimp postlarvae underwent a 5 C increase in acclimation temperature, resistance times tended to increase slightly after the initial (3-4 day) acclimation period (Fig. 20 and 21). Statistical analyses of an orthogonal polynomial fitted to data from these experiments indicated that the X_1 (linear) term was significant at both 1- and 2-day intervals for postlarvae tested at 38.7 C, and at 1-day intervals for postlarvae tested at 38.3 C. The X_1 term at 2-day intervals for postlarvae tested at 38.3 C, while not significant, was very close

to the 0.05 significance level. Since a significant X_1 term indicates a linear increase in resistance time (Y) over the range of times after transfer (X) (Van Der Reyden, 1943), it would appear that resistance time increased over the entire period of these experiments. While most of the acclimation by brown shrimp postlarvae to a 5 C increase in temperature was completed in 3-4 days, some acclimation continued to occur for 14 (and possibly 22) days.

The X_1 terms in orthogonal polynomials fitted to the data from the experiment involving a 9 C increase in acclimation temperature were not significant at either 1- or 2-day intervals. It appears, thus, that brown shrimp postlarvae undergoing a 9 C increase in acclimation temperature do not undergo a further increase in acclimation after the initial 4-day period.

Brown shrimp postlarvae apparently acclimated to a 5 C decrease in temperature by a rapid increase in acclimation, followed by a slower, steady increase to the new level. Acclimation to a 9 C increase in acclimation temperature, on the other hand, was accomplished by a rapid increase in acclimation which tended to overshoot the new level of acclimation, followed by a return to the new level. Thus, it appears that the rate of acclimation is affected by the amount of increase in the acclimation temperature, but not by the lethal temperature used.

During the first 4 days, acclimation increased most rapidly during the first 3 hours after transfer to the higher acclimation temperature

in all experiments on brown shrimp postlarvae involving an increase in acclimation temperature (Figs. 23, 24 and 25). After 3 hours, the postlarvae continued to acclimate at a somewhat slower rate for 3-4 days (Fig. 23, 24 and 25).

In all of the experiments involving increases in acclimation temperature, the resistance times were observed to fluctuate after the initial period of acclimation had been completed (Fig. 20, 21, and 22). In order to study these fluctuations, orthogonal polynomials were fitted to the data, using the least-squares method for determining the polynomial which best fit the data (Van Der Reyden, 1943).

For the experiment in which brown shrimp postlarvae were subjected to a 5 C increase in acclimation temperature (25 to 30 C) and tested at 38.7 C, a sixth degree polynomial was found to give the best fit when 2-day intervals were used, and a fifth degree polynomial gave the best fit when 1-day intervals were used. A sixth degree polynomial was fitted to the means of the data from this experiment (Fig. 26).

A fourth degree polynomial gave the best fit to the data from the experiment in which brown shrimp postlarvae were subjected to a 5 C increase in acclimation temperature (25 to 30 C) and tested at 38.3 C, when 2-day intervals were used, and a third degree polynomial gave the best fit when 1-day intervals were used. A fourth degree polynomial was fitted to the means of the data from this experiment (Fig. 27).

FIGURE 23.--Mean thermal resistance times for the first 4 days after transfer to 30 C for brown shrimp postlarvae originally acclimated at 25 C and tested at 38.7 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 4 days after transfer.

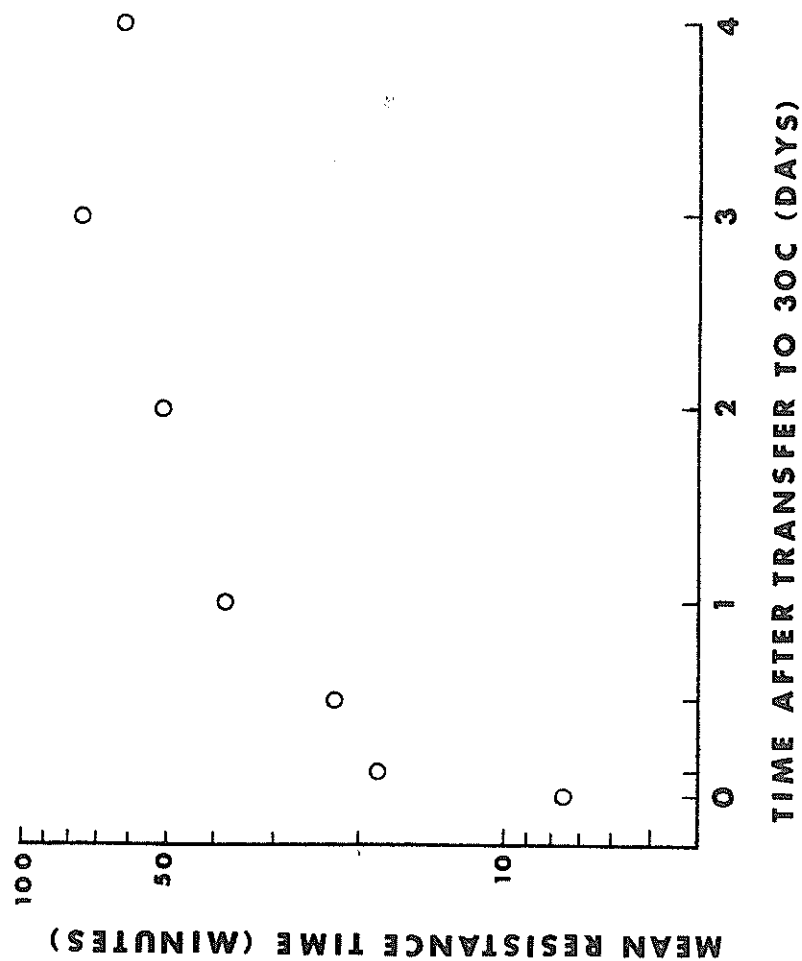


FIGURE 24. --Mean thermal resistance times for the first 4 days after transfer to 30 C for brown shrimp postlarvae originally acclimated at 25 C and tested at 38.3 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 4 days after transfer.

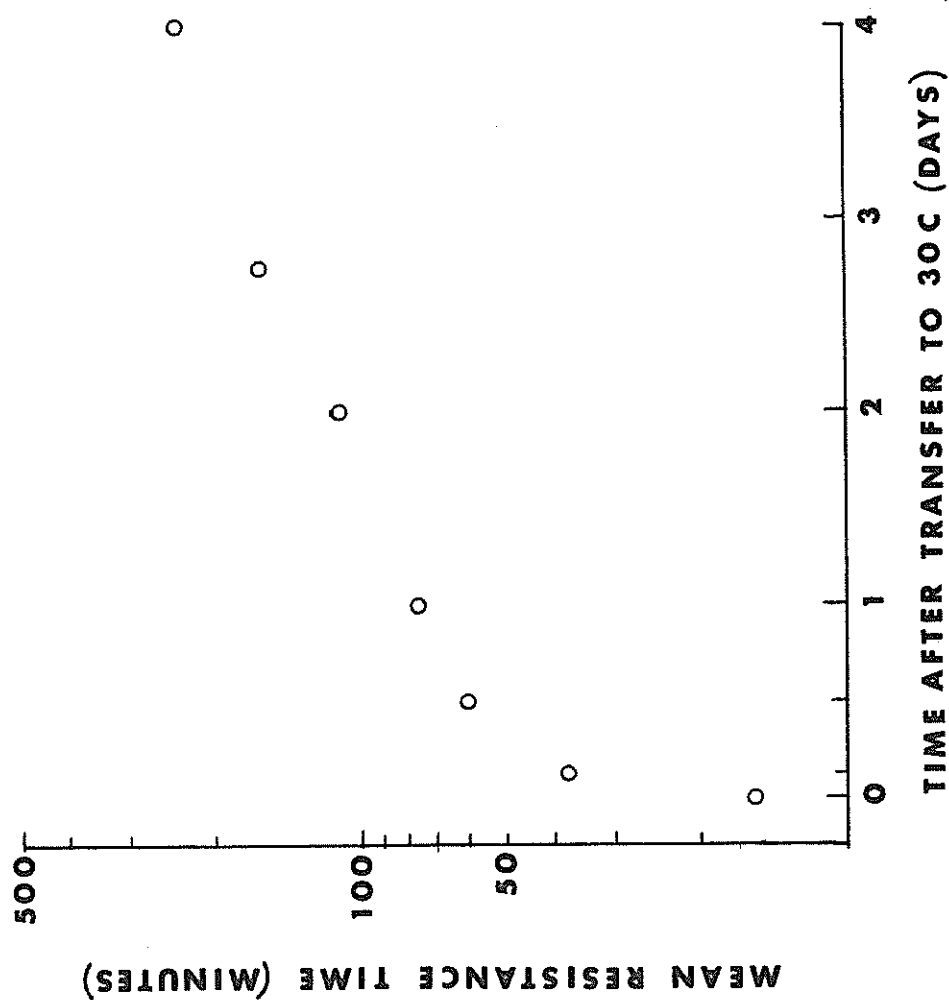


FIGURE 25.--Mean thermal resistance times for the first 4 days after transfer to 34 C for brown shrimp postlarvae originally acclimated at 25 C and tested at 39.5 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 4 days after transfer.

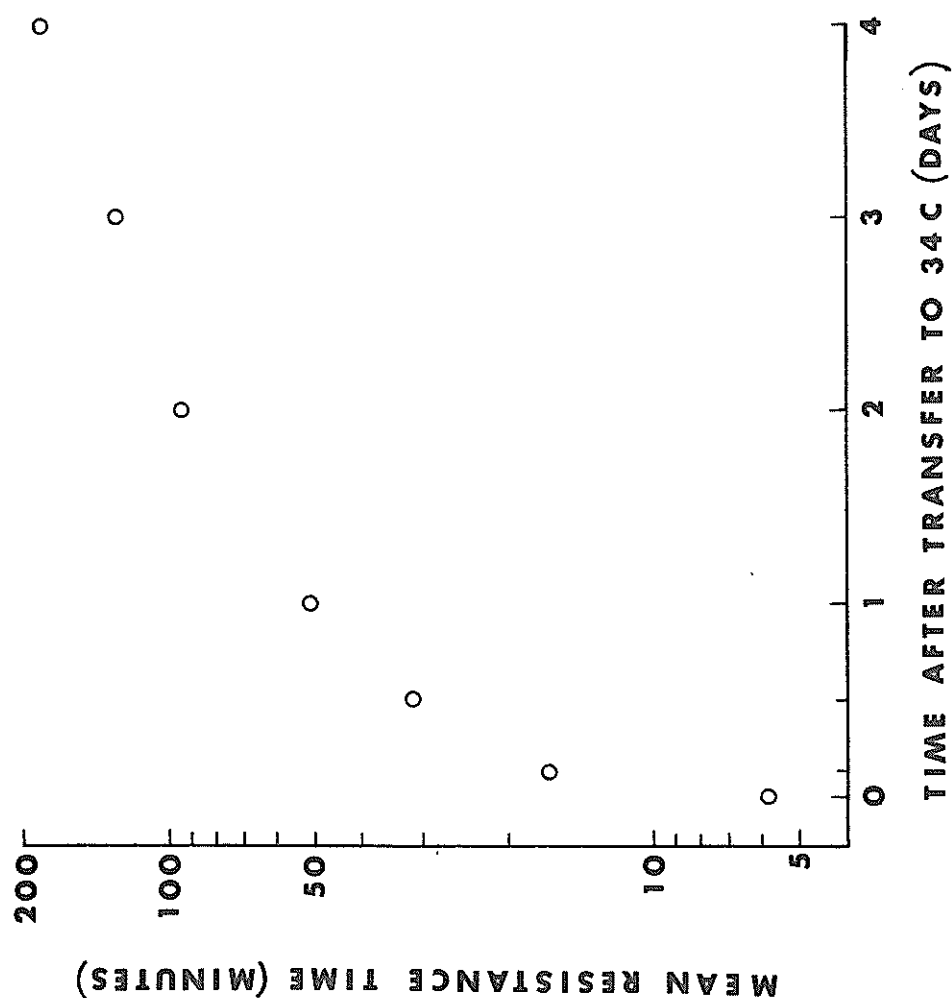


FIGURE 26.--Mean thermal resistance times for the entire experiment in which brown shrimp postlarvae were acclimated at 25 C, transferred to 30 C, and tested at 38.7 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 16 days after transfer; and 2-day intervals from 16 to 22 days after transfer. The line was fitted using a 6th degree polynomial.

FIGURE 26

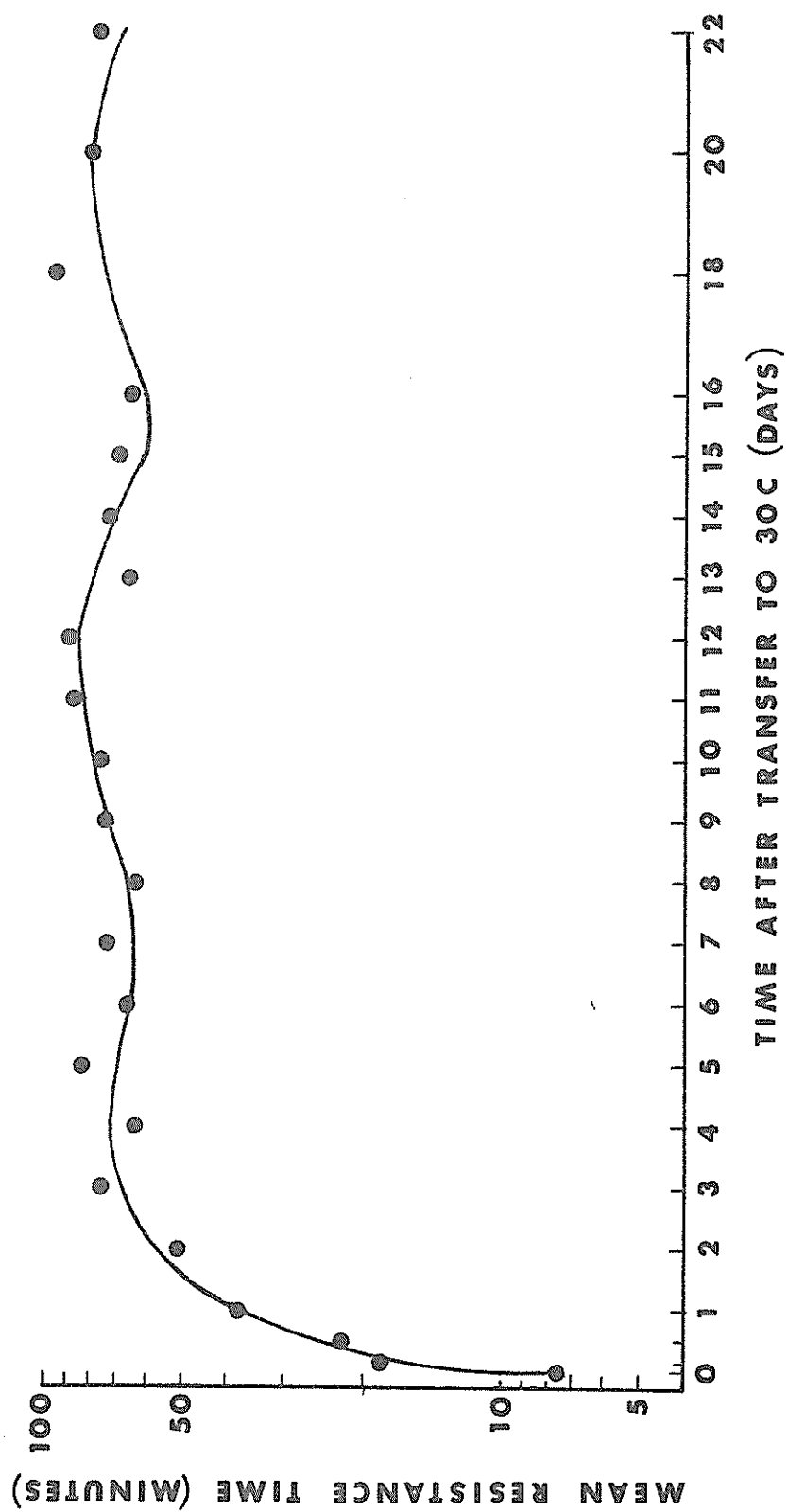
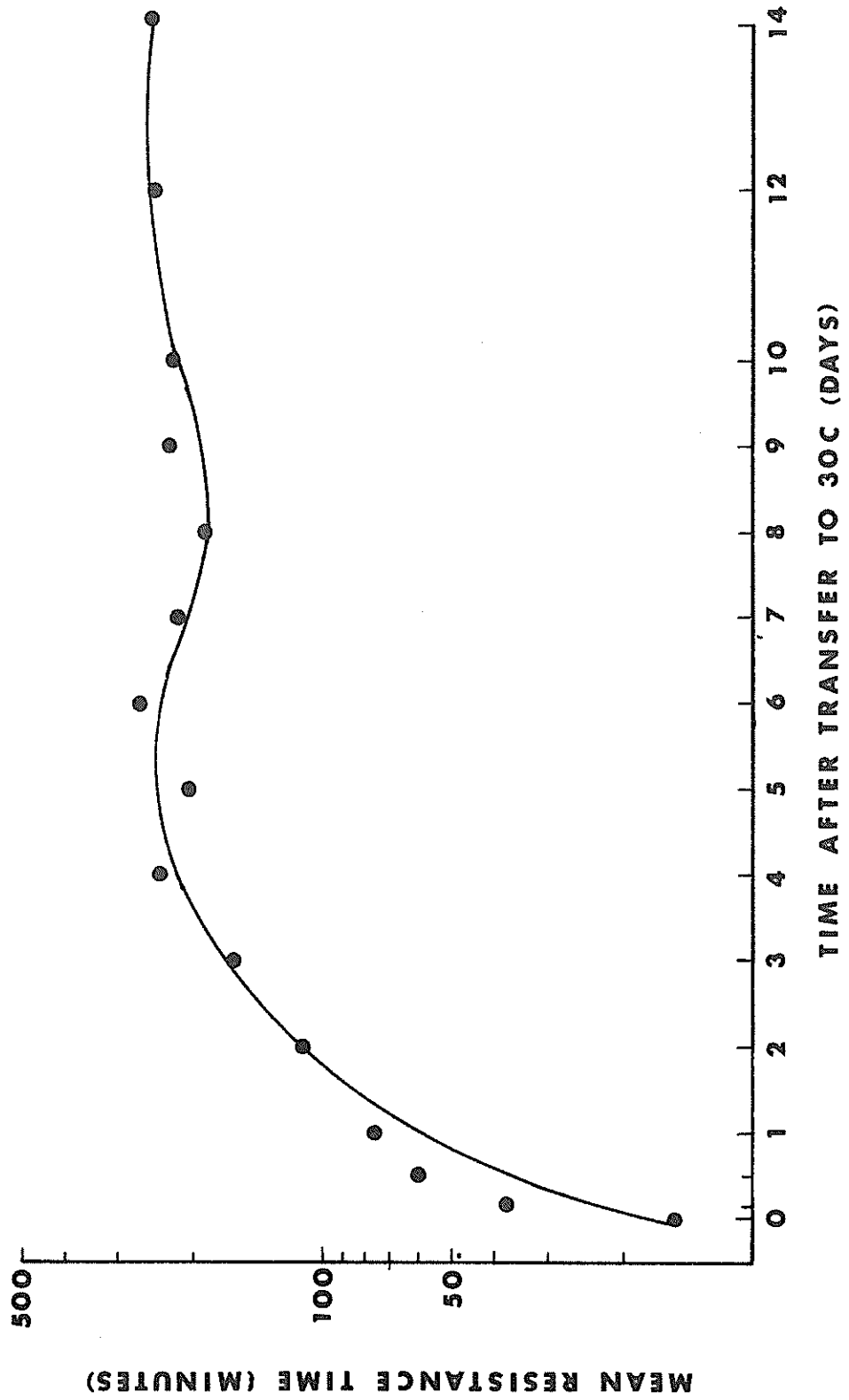


FIGURE 27.--Mean thermal resistance times for the entire experiment in which brown shrimp postlarvae were acclimated at 25 C, transferred to 30 C, and tested at 38.7 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 10 days after transfer; and 2-day intervals from 10 to 14 days after transfer. The line was fitted using a 4th degree polynomial.

FIGURE 27



In the experiment in which brown shrimp postlarvae were subjected to a 9 C increase in acclimation temperature (25 to 34 C), a fourth degree polynomial was the best fit when 2-day intervals were used. A fourth degree polynomial was fitted to the means of the data from this experiment (Fig. 28). A third degree polynomial gave the best fit when 1-day intervals were used.

These polynomials indicate the presence of a regularly recurring fluctuation in thermal resistance which is similar in all experiments (Fig. 26, 27, and 28). The first peak, or high point in thermal resistance, coincides with the completion of the initial period of acclimation at 4 days (Fig. 26, 27 and 28). Thereafter, peaks occur at approximately 8-day intervals (Fig. 26, 27 and 28).

An examination of the data indicates that the days on which the mean resistance time is greatest do not always coincide with the peaks predicted by the fitted line (Fig. 27 and 28). Observed peaks occurred at 5, 12, and 18 days in the experiment involving a 5 C increase in acclimation temperature and 38.7 C lethal temperature, at 6 and 14 days in the experiment involving a 5 C increase in acclimation temperature and 38.3 C lethal temperature, and at 4 and 10 days in the experiment involving a 9 C increase in acclimation temperature (Fig. 26, 27, and 28).

The individual resistance times of brown shrimp postlarvae which were subjected to a 5 C decrease in acclimation temperature (from 29 to 24 C) are shown in Figure 29. The two replications are combined,

FIGURE 28.--Mean thermal resistance times for the entire experiment in which brown shrimp postlarvae were acclimated at 25 C, transferred to 34 C, and tested at 39.5 C. Tests were conducted at: just before transfer; 2, 12, and 24 hours after transfer; 1-day intervals from 1 to 10 days after transfer; and 2-day intervals from 10 to 14 days after transfer. The line was fitted using a 4th degree polynomial.

FIGURE 28

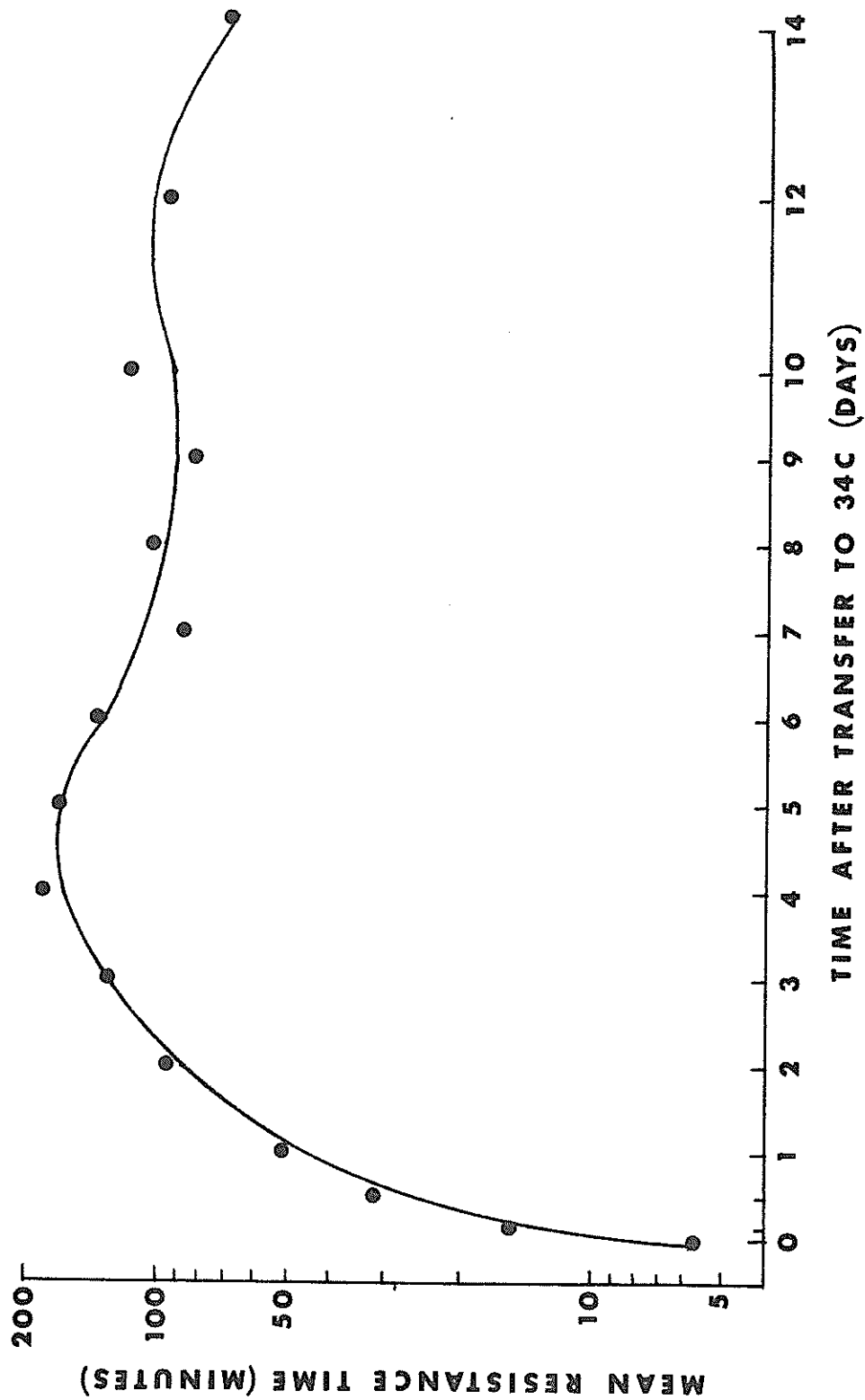
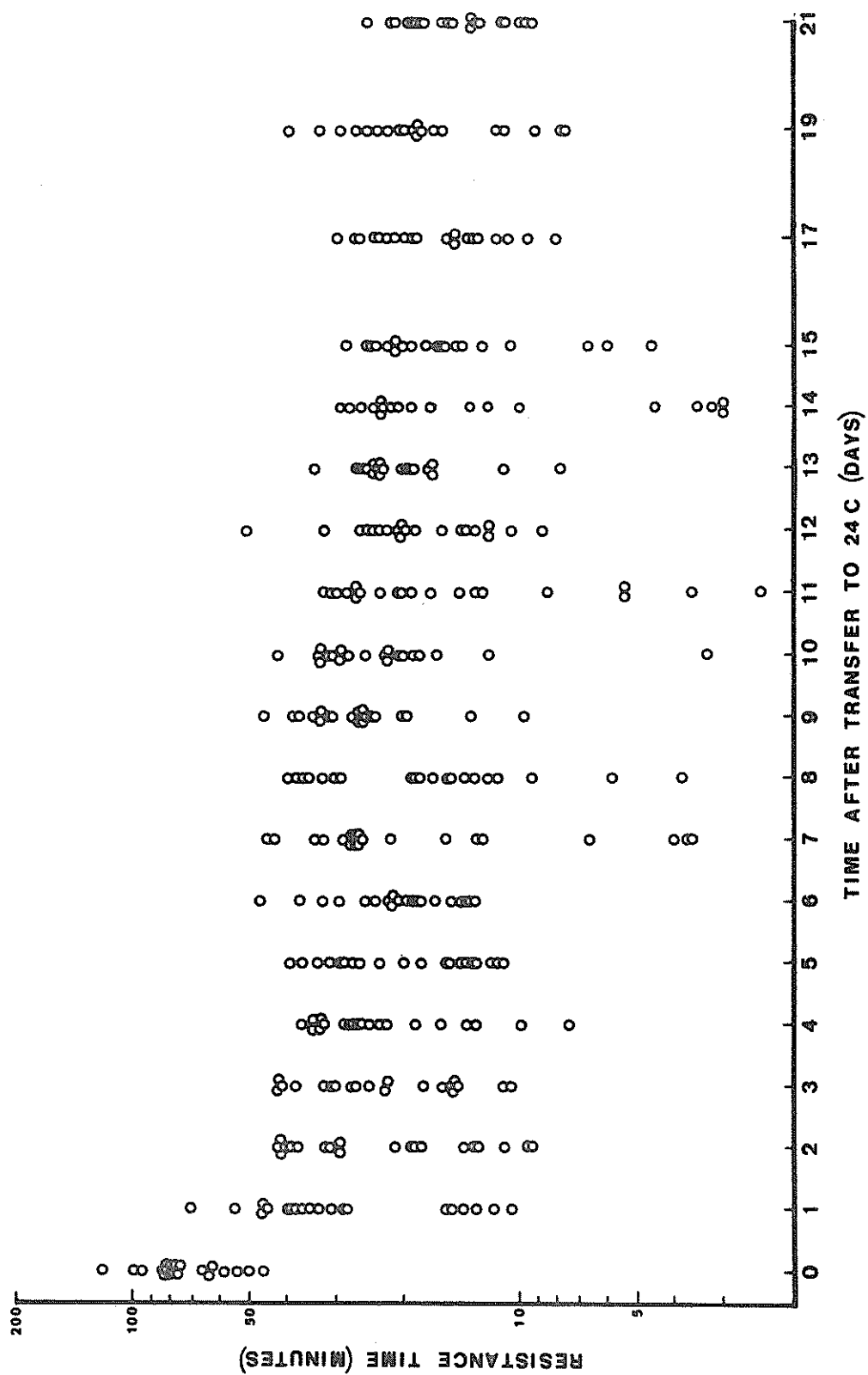


FIGURE 29.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 29 C, transferred to 24 C, and tested at 38.5 C. Tests were conducted at: just before transfer; 1-day intervals from 1 to 15 days after transfer; and 2-day intervals from 15 to 21 days after transfer. There were 20 postlarvae per test.

FIGURE 29



as there were no significant differences between replications.

The brown shrimp postlarvae lost thermal resistance at a fairly rapid rate for the first 2 days after transfer to 24 C (Fig. 29). Thereafter, resistance time declined slowly over the remainder of the experiment, as indicated by the significant X_1 terms in the statistical analysis of an orthogonal polynomial fitted to the data. Acclimation was apparently incomplete, even after 21 days; thus, acclimation to a decrease in temperature required a longer period of time than acclimation to an increase in temperature.

The least squares method was used to fit orthogonal polynomials to the data from this experiment. At 2-day intervals, a first degree or linear polynomial gave the best fit, and at 1-day intervals, a third degree polynomial was found to fit the data. Both the first and third polynomials are fitted to the means of the data in Figure 30. It appears that the fluctuations which were found in the experiments involving increases in temperature were not as well defined in this experiment.

White Shrimp Postlarvae

The individual resistance times of white shrimp postlarvae which were subjected to a 5 C increase in acclimation temperature (29 to 34 C) and tested at a lethal temperature of 40 C are shown in Figure 31. There were no significant differences between replications so they were combined. The postlarvae underwent a fairly rapid increase in

FIGURE 30.--Mean thermal resistance times of brown shrimp post-larvae acclimated at 29 C, transferred to 24 C, and tested at 38.5 C. Tests were conducted at: just before transfer; 1-day intervals from 1 to 15 days after transfer; and 2-day intervals from 15 to 21 days after transfer. The lines were fitted using a 1st degree (dashed line) and a 3rd degree (solid line) polynomial.

FIGURE 30

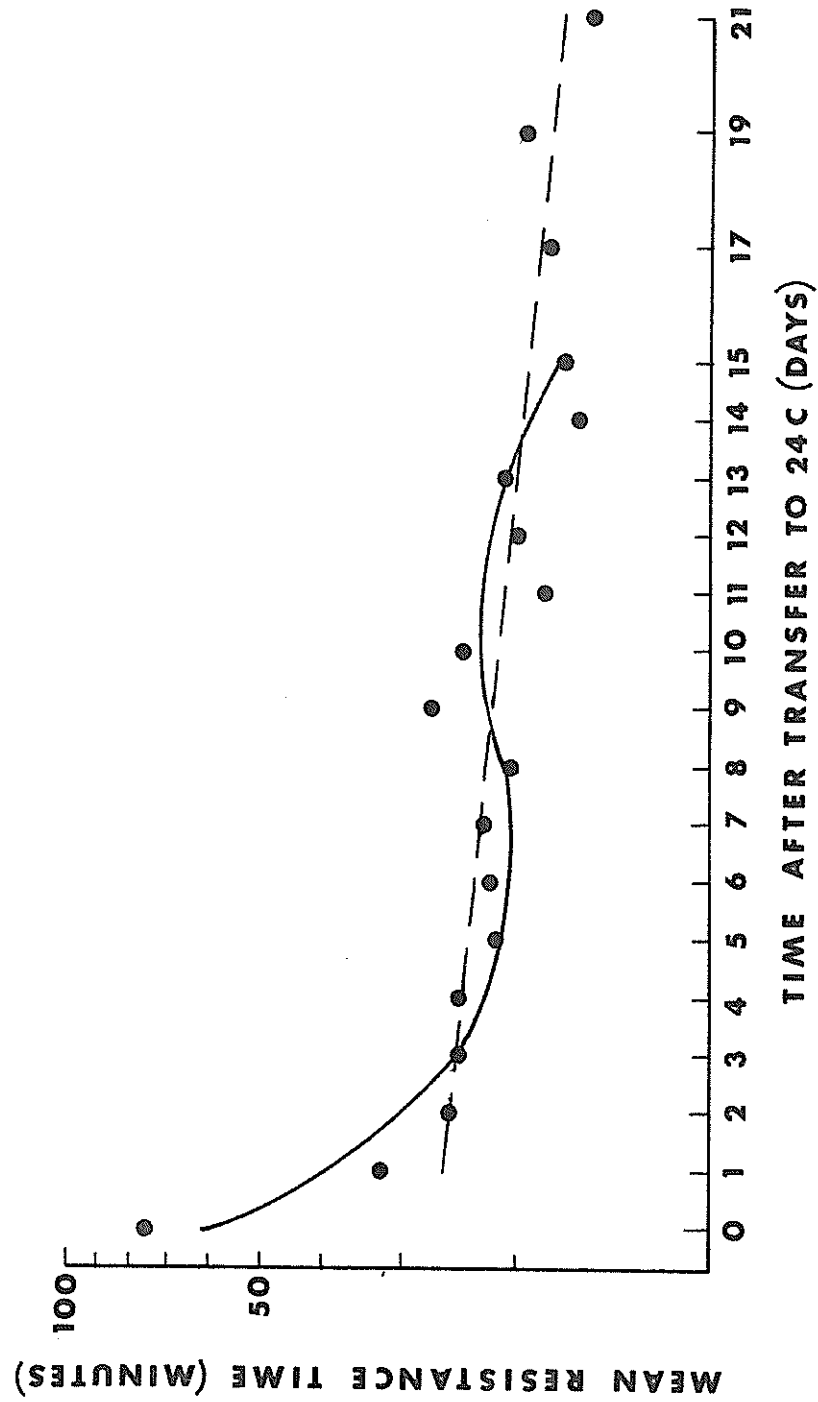
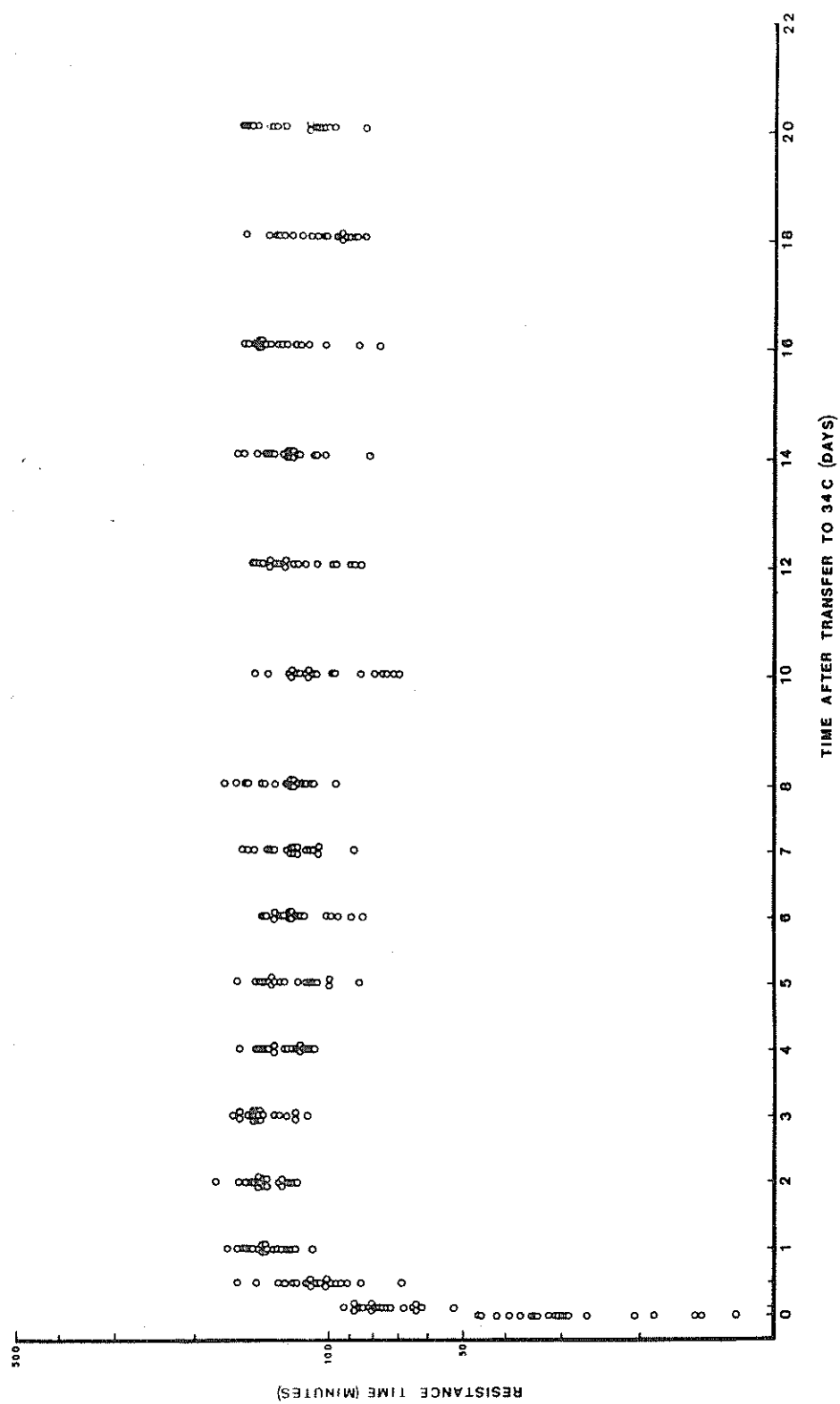


FIGURE 31.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C, transferred to 34 C, and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 8 days after transfer; and 2-day intervals from 8 to 22 days after transfer. There were 20 shrimp per test.

FIGURE 31



thermal resistance during the first day after transfer, after which there was no apparent increase in resistance time over the period of the experiment (Fig. 31). The X_1 term of an orthogonal polynomial fitted to the data was not significant at either 1- or 2-day intervals, also indicating that no general increase in thermal resistance occurred after the initial (1-day) acclimation period. Thus, it appears that white shrimp postlarvae acclimated to these conditions in 1 day.

The individual resistance times of white shrimp postlarvae which were subjected to an 8 C increase in acclimation temperature (27 to 35 C) and tested at 40 C are given in Figure 32. There was no statistically significant difference between replications, so they were combined.

Acclimation to an 8 C increase in temperature in white shrimp postlarvae proceeded at a fairly rapid rate for the first 2 days after transfer, after which no further increase occurred (Fig. 32). The X_1 terms of an orthogonal polynomial fitted to the data were not significant at either 1- or 2-day intervals, indicating that no increase in thermal resistance occurred after the initial (2-day) period of acclimation.

The individual resistance times of white shrimp postlarvae which were subjected to a 5 C increase in acclimation temperature (29 to 34 C) and tested at 39.3 C are shown in Figure 33. No significant difference between replications was found, so the two replications were combined.

Most of the acclimation to the temperature increase was apparently complete in 12 hours, although the greatest thermal resistance

FIGURE 32.--Individual thermal resistance times of white shrimp postlarvae acclimated at 27 C, transferred to 35 C, and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 8 days after transfer; and 2-day intervals from 8 to 14 days after transfer. There were 20 postlarvae per test.

FIGURE 32

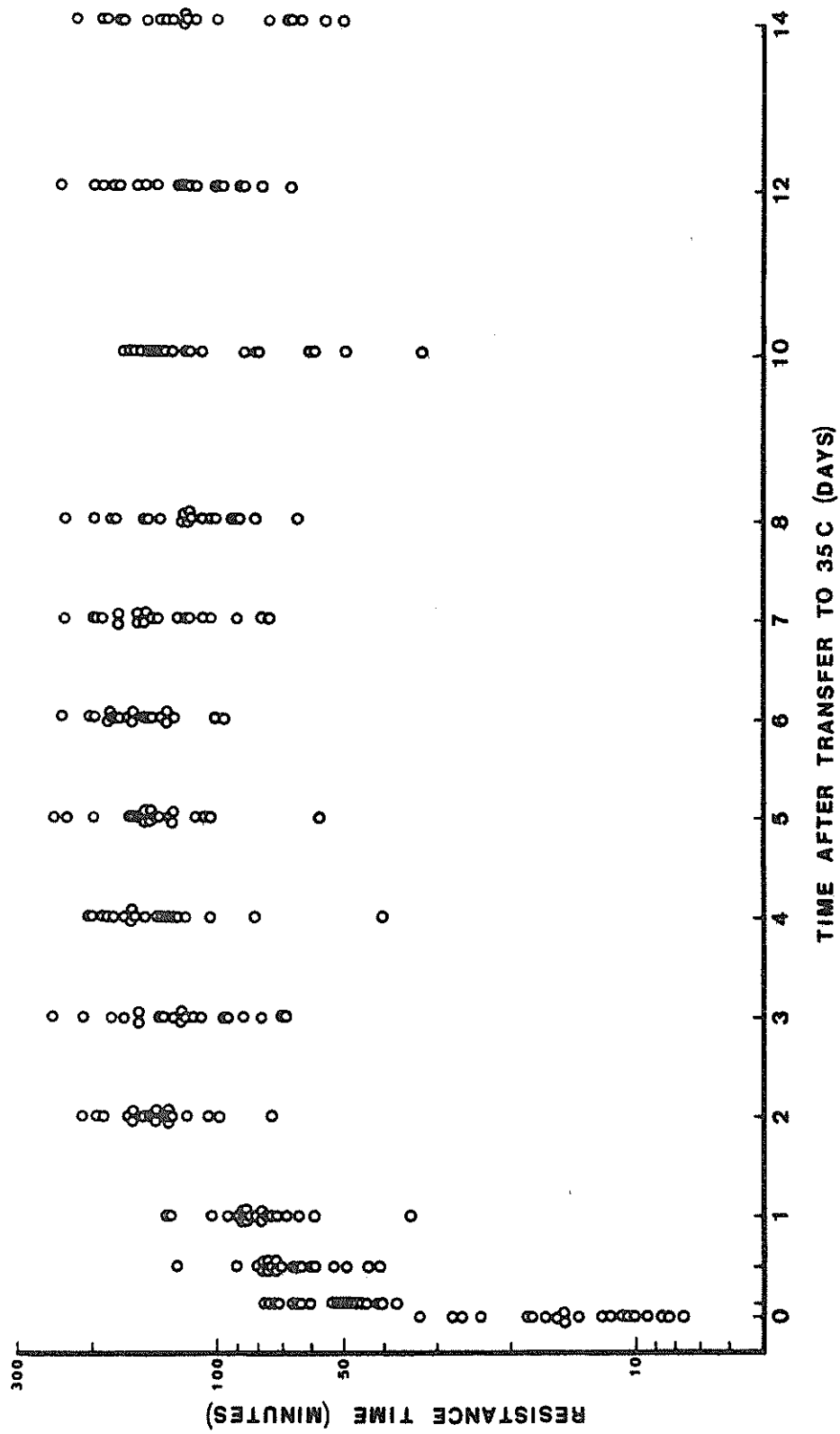
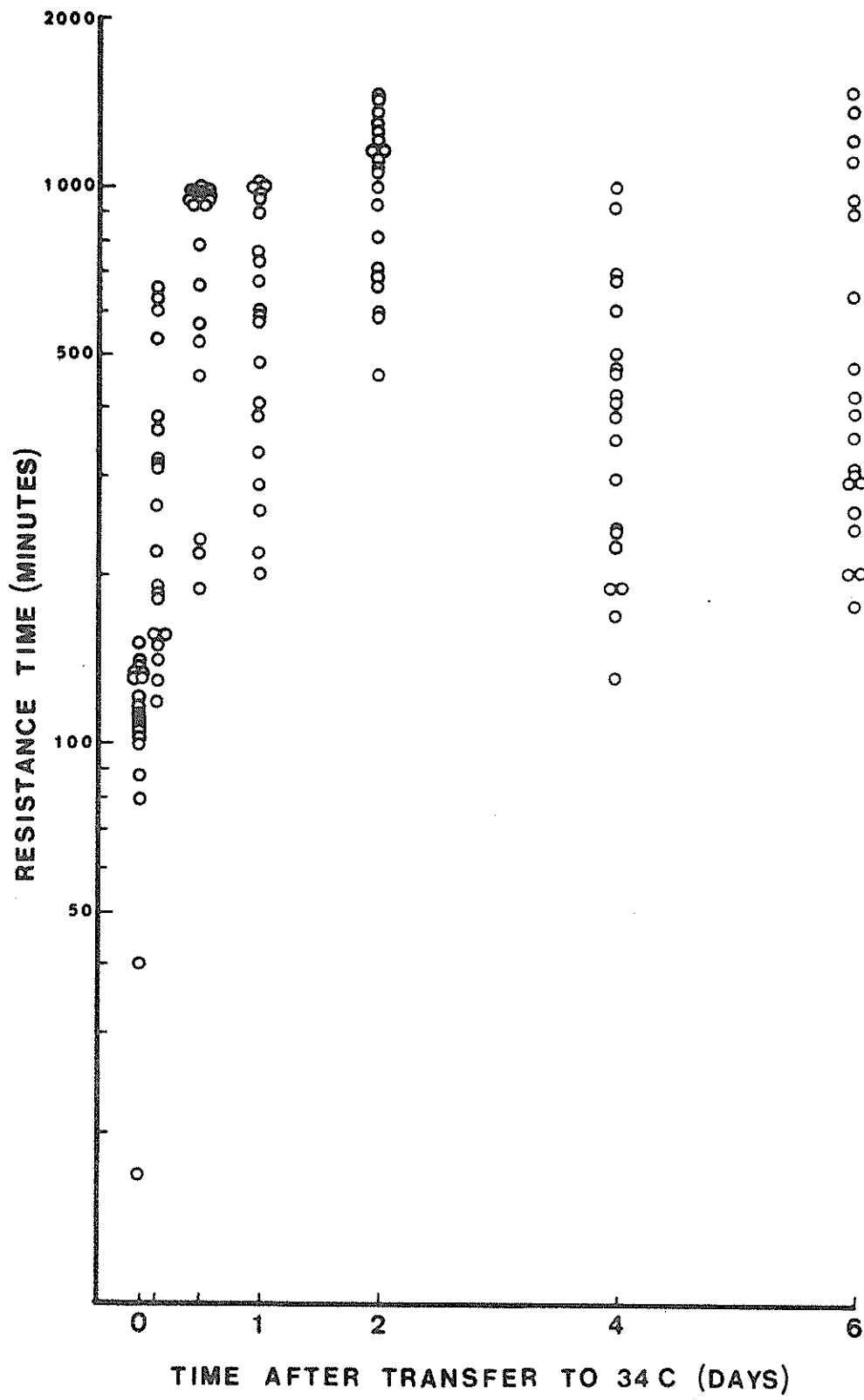


FIGURE 33.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C, transferred to 34 C, and tested at 39.3 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 2, 4, and 6 days after transfer. There were 20 shrimp per test.

FIGURE 33



was achieved on the second day (Fig. 33). The postlarvae apparently overshot the new level of acclimation, as thermal resistance declined after the second day (Fig. 33). The pattern of acclimation in this experiment differed from that of the experiment involving a 5 C increase in temperature (29 to 34 C) and a lethal temperature of 40 C (Fig. 31).

During the initial period of acclimation, thermal resistance increased most rapidly during the first 3 hours in white shrimp postlarvae (Fig. 34, 35 and 36). After the first 3 hours, acclimation proceeded at a somewhat slower rate until complete acclimation was achieved (Fig. 34, 35, and 36).

In the white shrimp experiments involving an increase in acclimation temperature, as in the brown shrimp experiments, the resistance times were observed to fluctuate after the initial period of acclimation (Fig. 31, 32 and 33). Orthogonal polynomials were also fitted to the white shrimp data in order to study these fluctuations.

In the experiment in which white shrimp postlarvae were subjected to a 5 C increase in acclimation temperature and tested at 40 C, an eighth degree polynomial was found to be the best fit of the data when 2-day intervals were used. A fourth degree polynomial was the best fit when 1-day intervals were used. Both a fourth and an eighth degree polynomial are fitted to the means of the data from this experiment in Figure 37.

A sixth degree polynomial was the best fit of the data from the experiment in which white shrimp postlarvae were subjected to an 8 C

FIGURE 34.--Mean thermal resistance times for the first 4 days after transfer to 34 C for white shrimp postlarvae originally acclimated at 29 C and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 4 days after transfer.

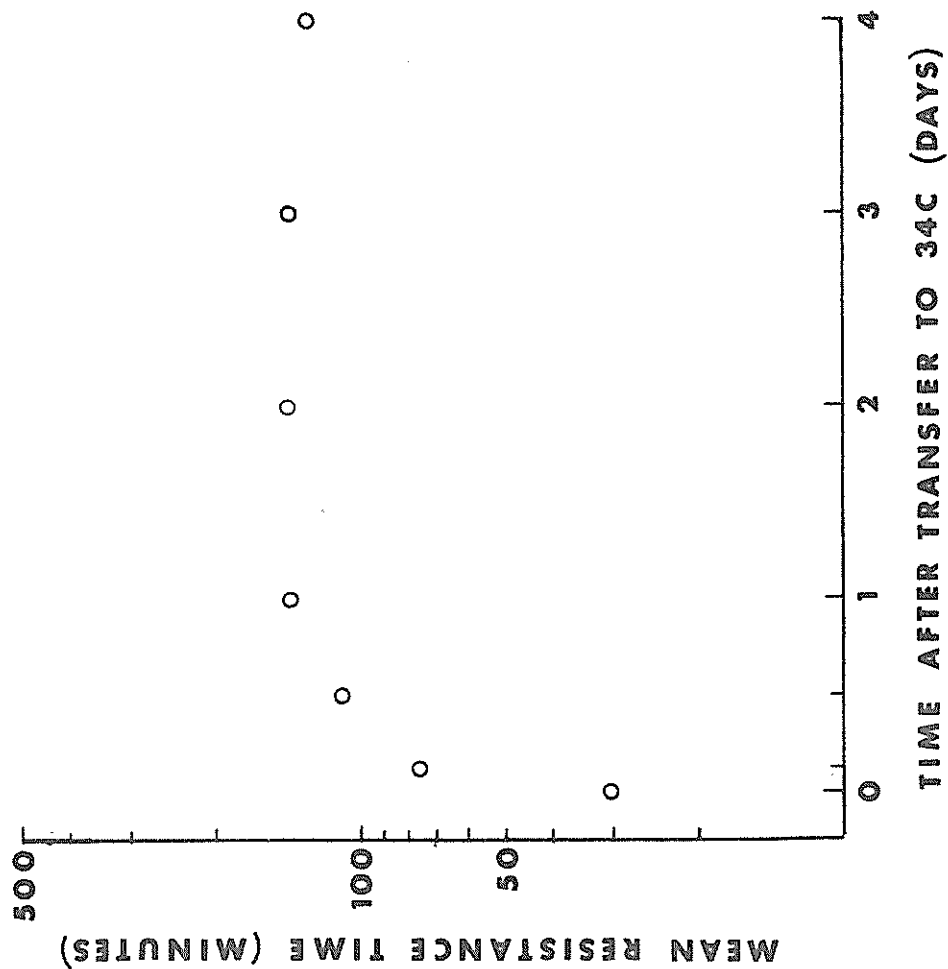


FIGURE 35.--Mean thermal resistance times for the first 4 days after transfer to 35 C for white shrimp postlarvae originally acclimated at 27 C and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 4 days after transfer.

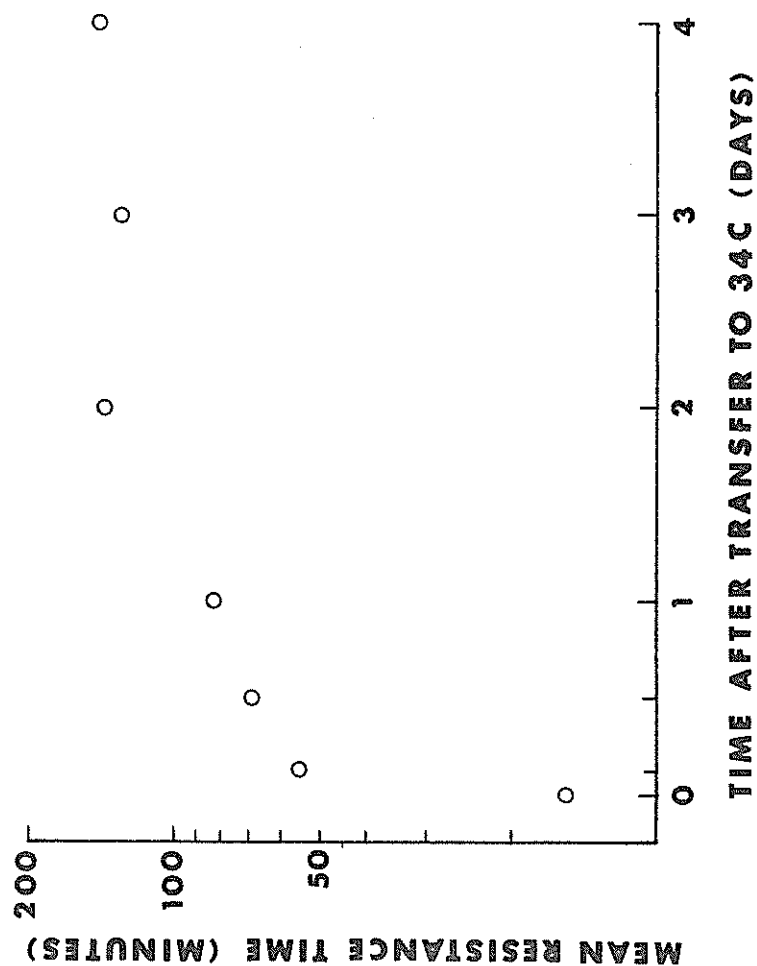


FIGURE 36.--Mean thermal resistance times for the entire experiment in which white shrimp postlarvae were acclimated at 29 C, transferred to 34 C, and tested at 39.3. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and at 2, 4, and 6 days after transfer.

FIGURE 36

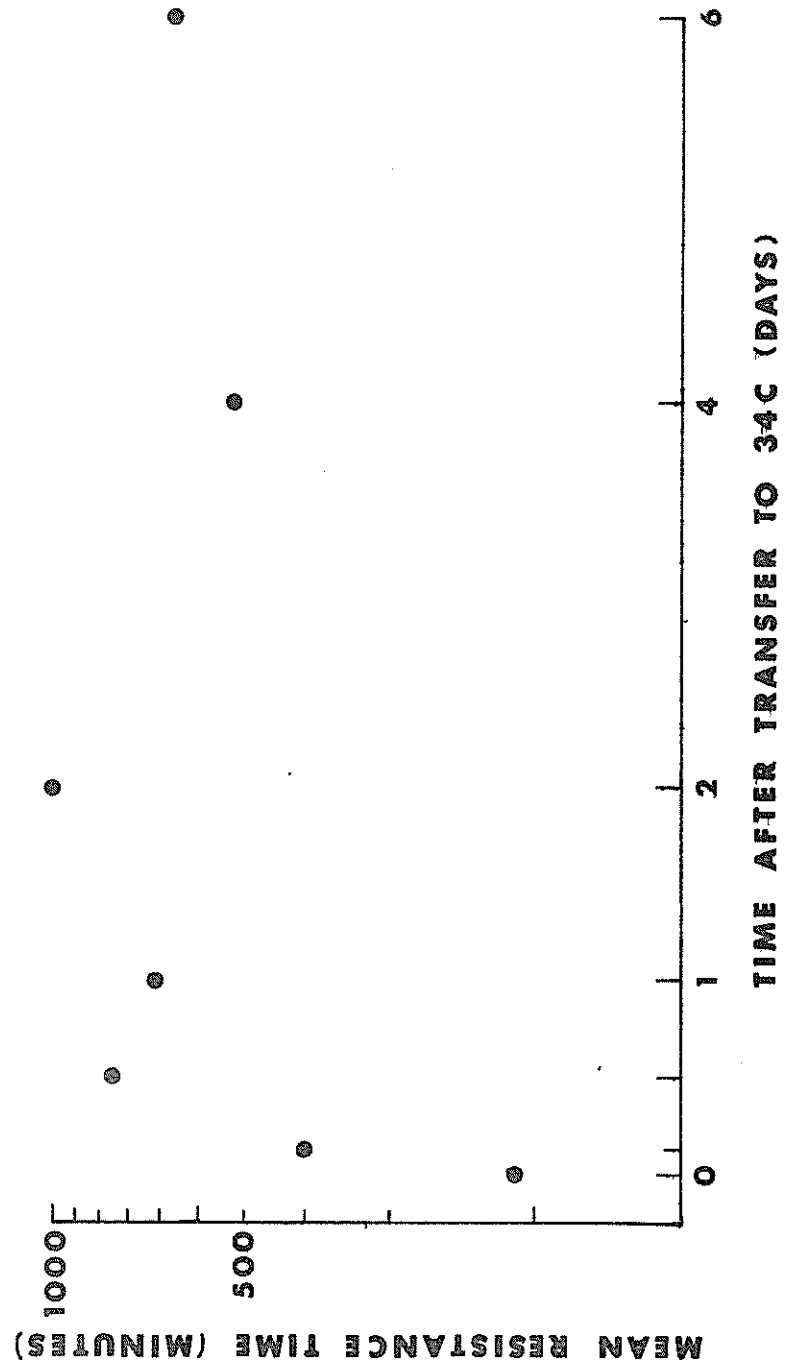
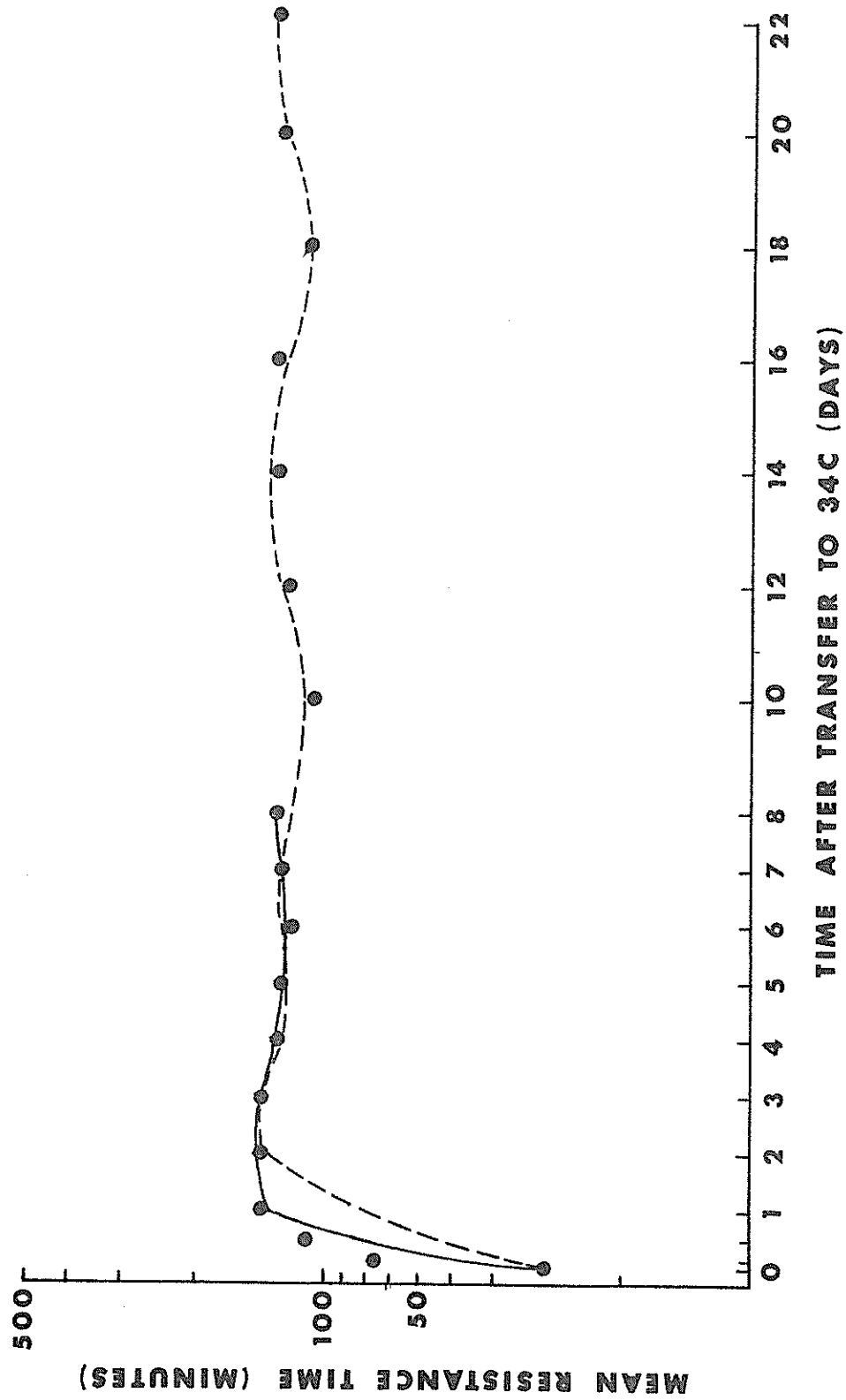


FIGURE 37.--Mean thermal resistance times for the entire experiment in which white shrimp postlarvae were acclimated at 29 C, transferred to 34 C, and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 8 days after transfer; and 2-day intervals from 8 to 22 days after transfer. The lines were fitted using a 4th degree (solid line) and an 8th degree (dashed line) polynomial.

FIGURE 37

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increase in acclimation temperature, when 2-day intervals were used. A sixth degree polynomial was used to fit the line in Figure 38. A fifth degree polynomial gave the best fit when 1-day intervals were used.

Neither a first or a second degree polynomial fit the data from the experiment in which white shrimp postlarvae were subjected to a 5 C increase in acclimation temperature and tested at 39.3 C. Since a polynomial of $n-1$ degrees will always fit the data (Van Der Reyden, 1943), a third degree polynomial is probably the only one that would fit the data from this experiment.

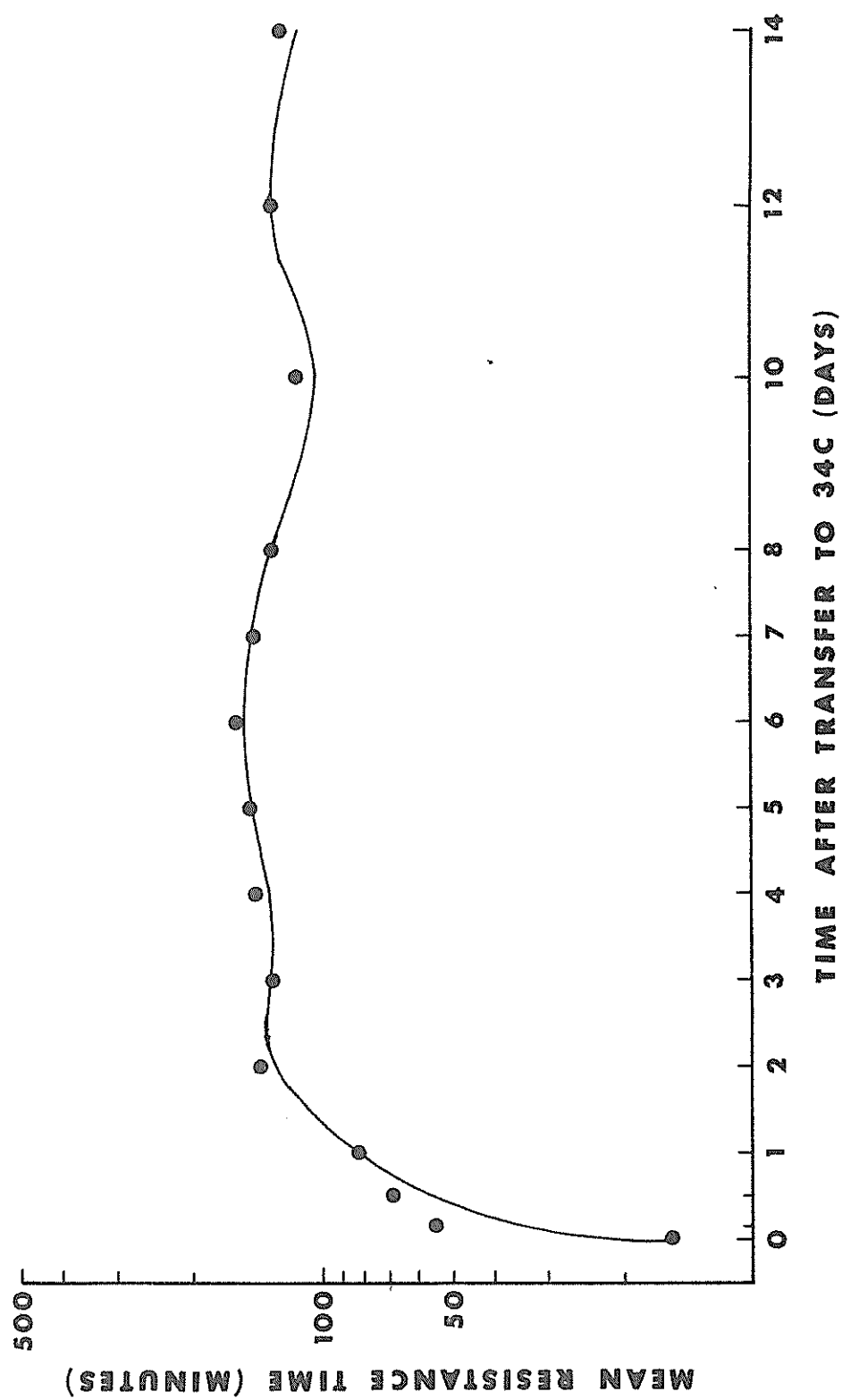
Both the fitted line and the mean resistance times indicate a regularly recurring fluctuation in thermal resistance in the experiment in which white shrimp postlarvae were subjected to a 5 C increase in temperature and tested at 40 C (Fig. 37). The peaks of thermal resistance seemed to occur at approximately 6-day intervals (Fig. 37).

It appears that the fluctuations did not recur at regular intervals in the experiment in which white shrimp postlarvae were subjected to an 8 C increase in acclimation temperature (Fig. 38). There were 4 days between the first and second peaks, and 6 days between the second and third (Fig. 38). The experiment involving a 5 C increase in acclimation temperature and a lethal temperature of 39.3 C was too short (6 days) to provide any information on long-term fluctuations in thermal resistance.

The individual resistance times of white shrimp postlarvae which were subjected to a 5 C decrease in acclimation temperature (from 29

FIGURE 38.--Mean thermal resistance times for the entire experiment in which white shrimp postlarvae were acclimated at 27 C, transferred to 35 C, and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; 1-day intervals from 1 to 8 days after transfer; and 2-day intervals from 8 to 14 days after transfer. The line was fitted using a 6th degree polynomial.

FIGURE 38



to 24 C) are shown in Figure 39. The two replications are combined, as statistical analysis indicated that there were no significant differences between replications.

White shrimp postlarvae lost thermal resistance at a fairly rapid rate for the first 1-3 days after transfer to 24 C (Fig. 39). Thereafter, resistance time declined slowly over the remainder of the experiment, as indicated by the significant X_1 term in the statistical analysis of an orthogonal polynomial fitted to the data. Acclimation was apparently incomplete, even after 22 days (Fig. 39).

The least-squares method was used to fit an orthogonal polynomial to the data from this experiment. A fifth degree polynomial was found to be the best fit at 2-day intervals. The fifth degree polynomial was used to fit a line to the means of the data in Figure 40. The regularly recurring fluctuations in thermal resistance found in some of the experiments involving increases in temperature were apparently not present in this experiment.

Species Comparison

The individual resistance times of brown shrimp postlarvae, which were collected at the same time as the white shrimp postlarvae subjected to a 5 C temperature increase and acclimated and tested at the same temperatures, are shown in Figure 41. The two replications are combined in this figure because no significant differences between replications were found.

Thermal resistance in these postlarvae increased for the first 3

FIGURE 39.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C, transferred to 24 C, and tested at 38.8 C. Tests were conducted at: just before transfer; 1-day intervals from 1 to 6 days after transfer; and 2-day intervals from 6 to 22 days after transfer. There were 20 shrimp per test.

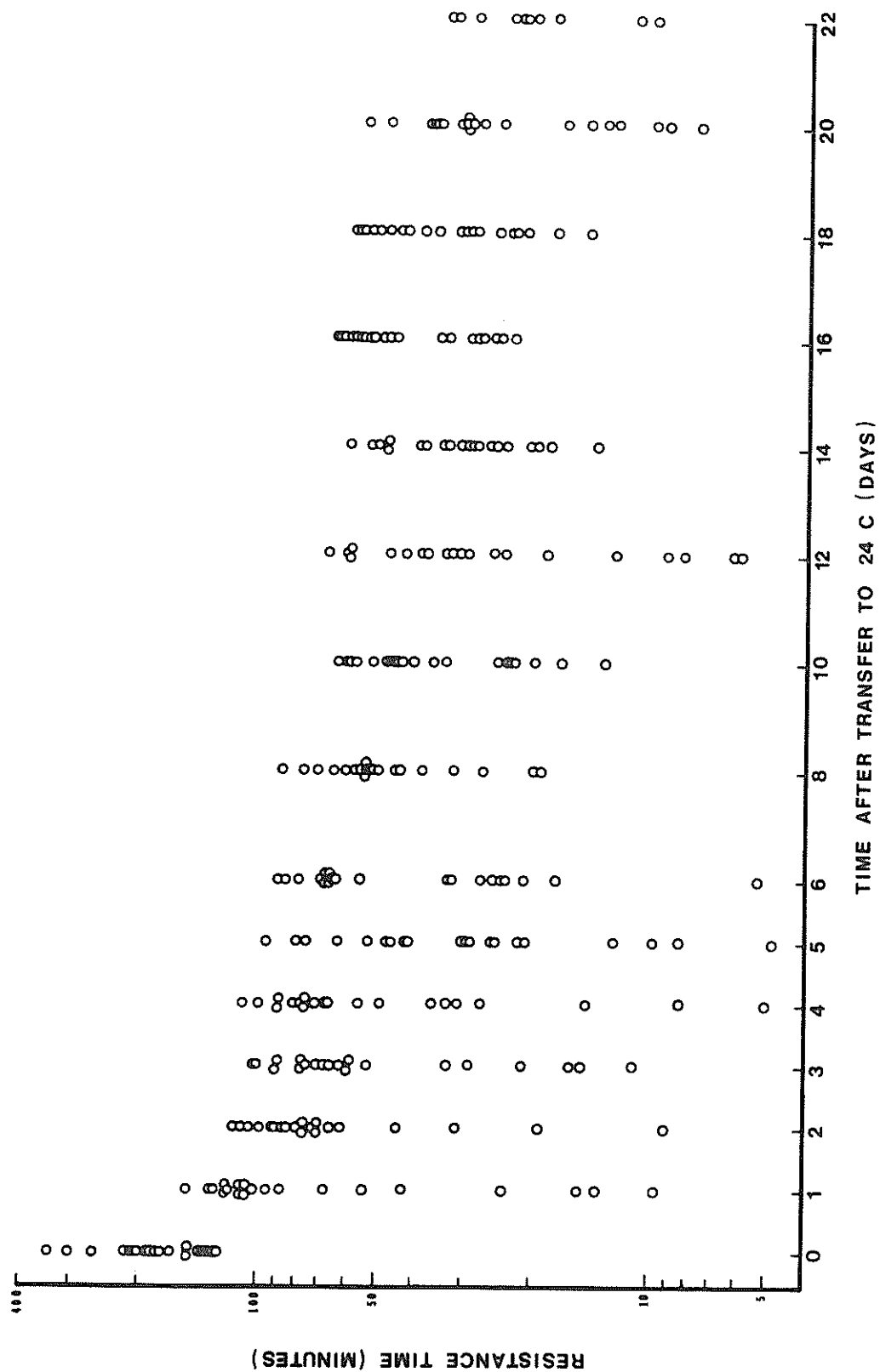


FIGURE 40.--Mean thermal resistance times of white shrimp post-larvae acclimated at 29 C, transferred to 24 C, and tested at 38.8 C. Tests were conducted at: just before transfer; 1-day intervals from 1 to 6 days after transfer; and 2-day intervals from 6 to 22 days after transfer. The line was fitted using a 5th degree polynomial.

FIGURE 40

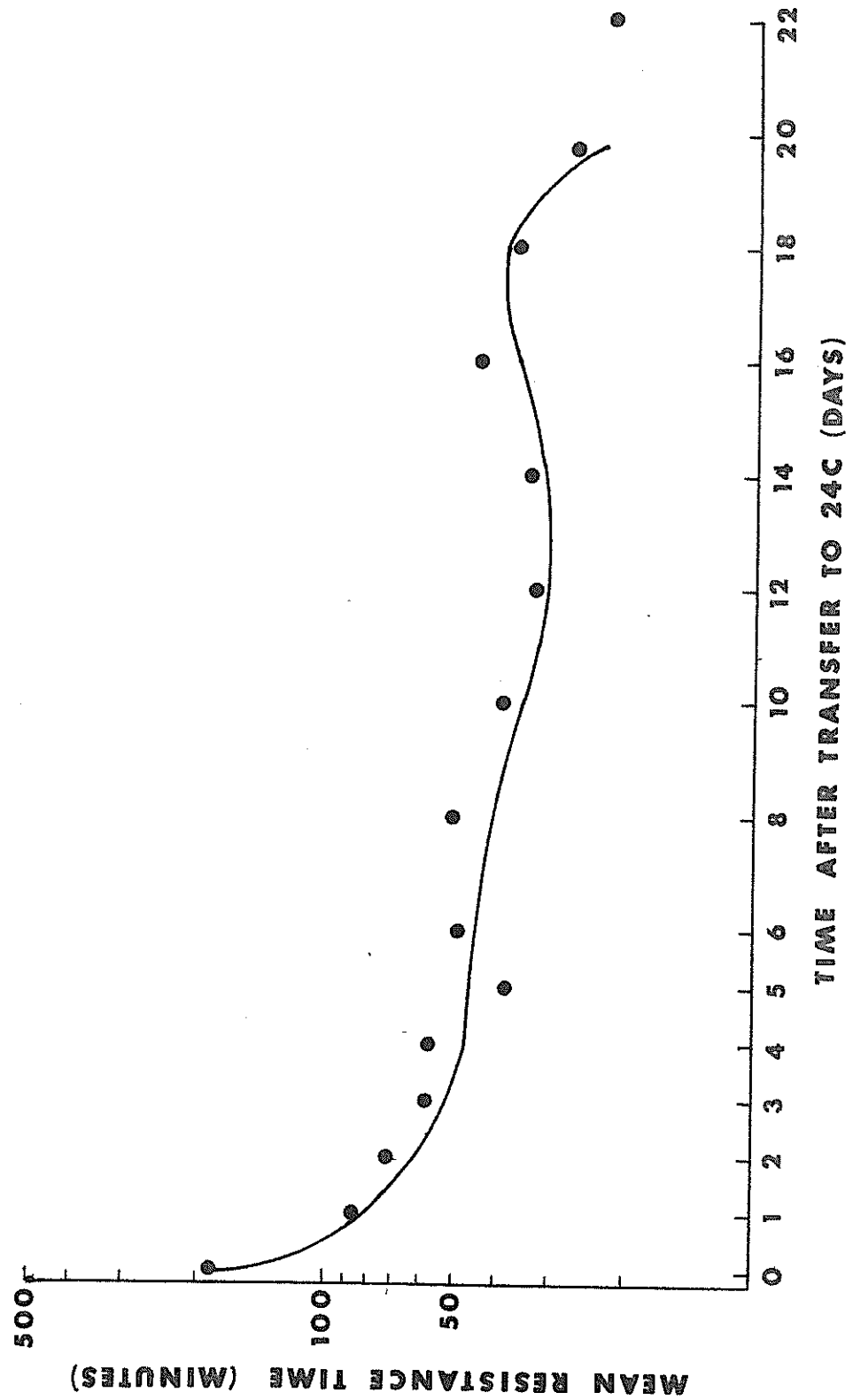
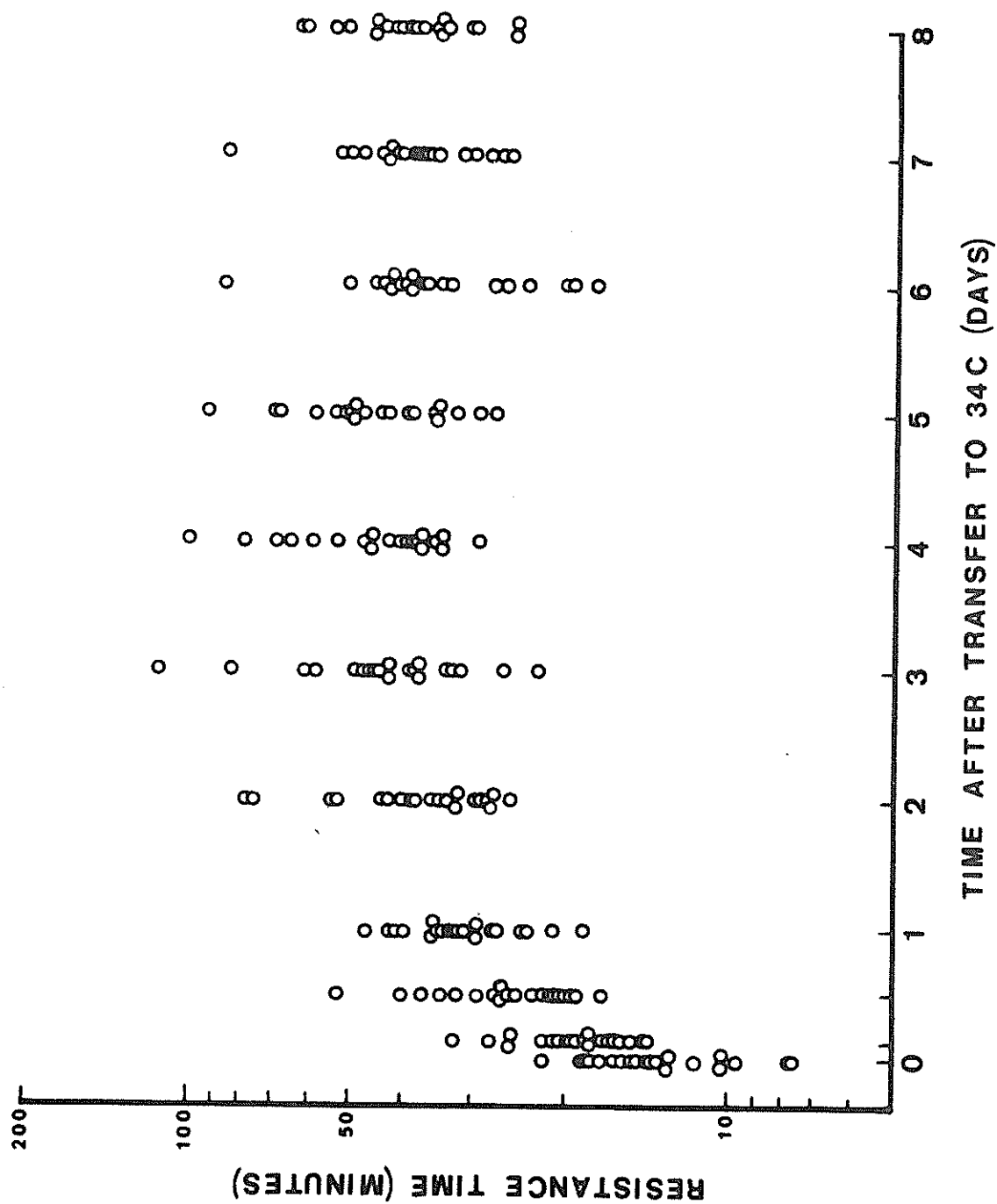


FIGURE 41.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 29 C, transferred to 34 C, and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 8 days after transfer. There were 20 shrimp per test.

FIGURE 41



days after transfer, after which there was no apparent increase in thermal resistance for the remainder of the experiment (Fig. 41).

A lack of increase in thermal resistance over the period of the experiment is also indicated by the non-significant X_1 term in an orthogonal polynomial fitted to the data.

A comparison of the mean resistance times of the white and brown shrimp postlarvae indicated that the white shrimp postlarvae acclimated to the temperature increase (29 to 34 C) much more rapidly than did the brown shrimp postlarvae (Fig. 42). Factorial analysis of the two experiments found a significant interaction between species and time after transfer, also indicating differences in the acclimation rates of the two species.

In both species, acclimation to a temperature increase was most rapid in the first 3 hours after transfer (Fig. 43). After 3 hours, acclimation increased at a somewhat slower rate in both species, until the new level of acclimation was reached. The data from the comparison study on brown shrimp postlarvae was best fit by a third degree polynomial. The third degree polynomial is fitted to the means of the data from the brown shrimp experiment in Figure 44.

The mean resistance times of white and brown shrimp postlarvae which underwent a 5 C decrease in acclimation temperature are compared in Figure 45. Both species responded to the decrease in temperature in a similar manner. A rapid loss of thermal resistance was followed by a slow decrease in thermal resistance over the period of the experiment. Factorial analysis of the two experiments found no

FIGURE 42.--A comparison of the mean thermal resistance times for white (Δ) and brown (O) shrimp postlarvae acclimated at 29 C, transferred to 34 C, and tested at 40 C for 8 days.

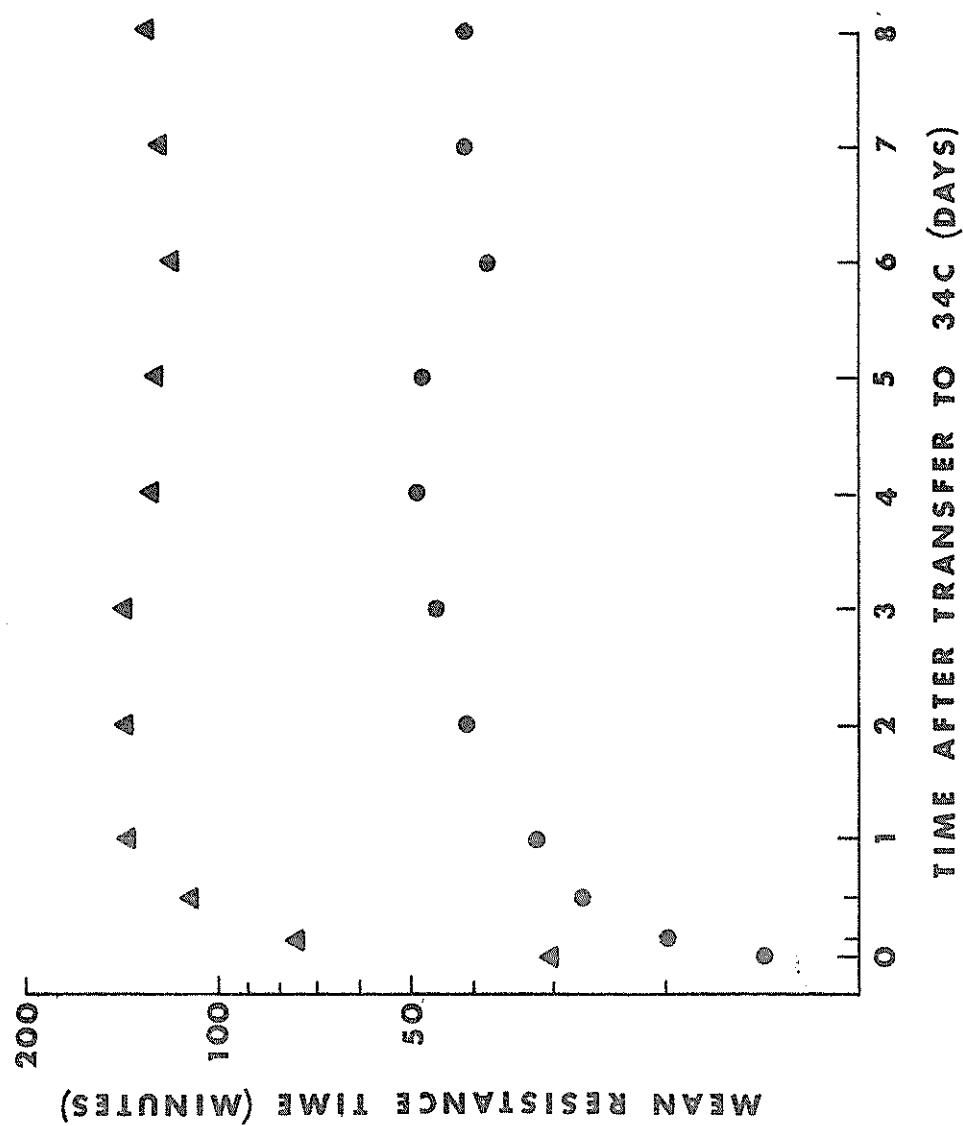


FIGURE 43.--Mean thermal resistance times for the first 4 days after transfer to 34 C for brown shrimp postlarvae originally acclimated at 29 C and tested at 40 C. Tests were conducted at: just before transfer; 3, 12, and 24 hours after transfer; and 1-day intervals from 1 to 4 days.

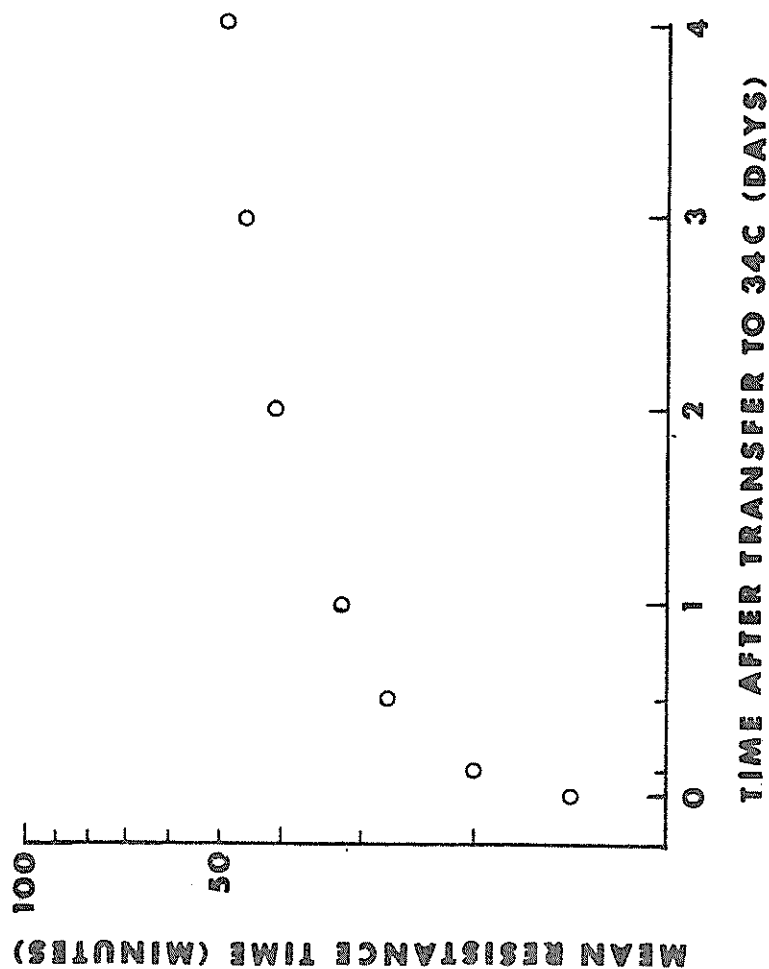


FIGURE 44.--Mean thermal resistance times for the entire experiment in which brown shrimp postlarvae were acclimated at 29 C, transferred to 34 C, and tested at 40 C. Tests were conducted at intervals from 1 to 8 days after transfer. The line was fitted using a 3rd degree polynomial.

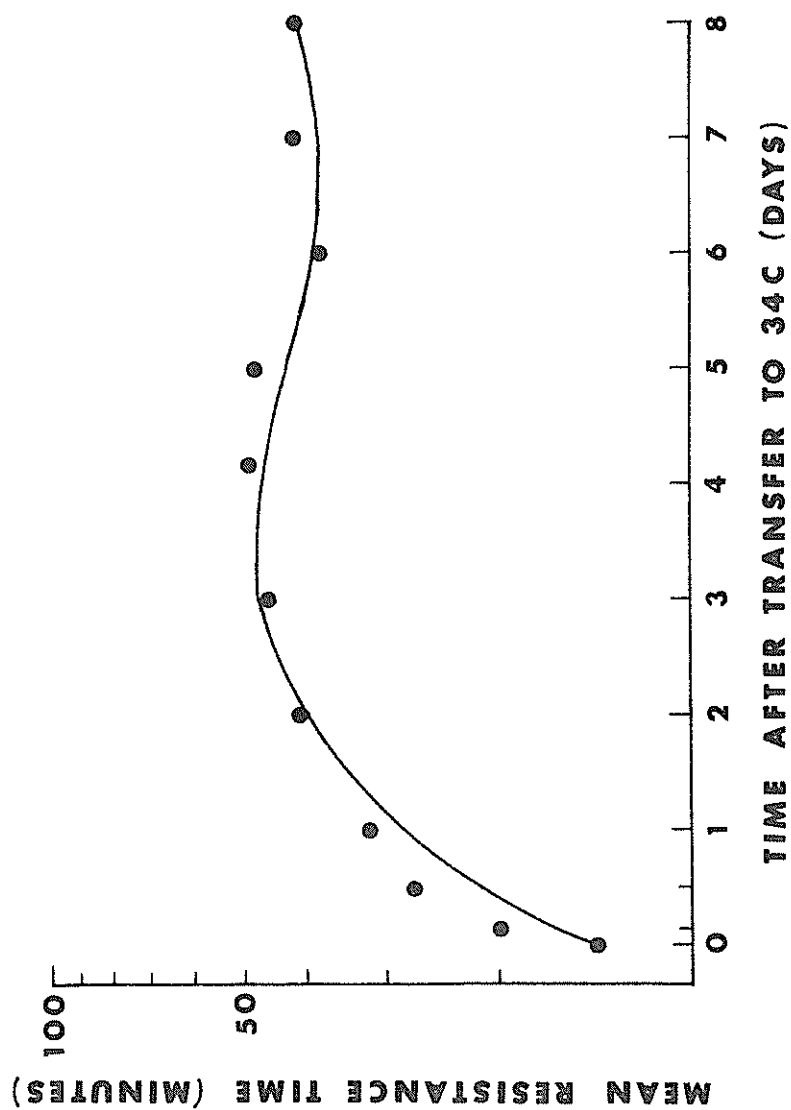
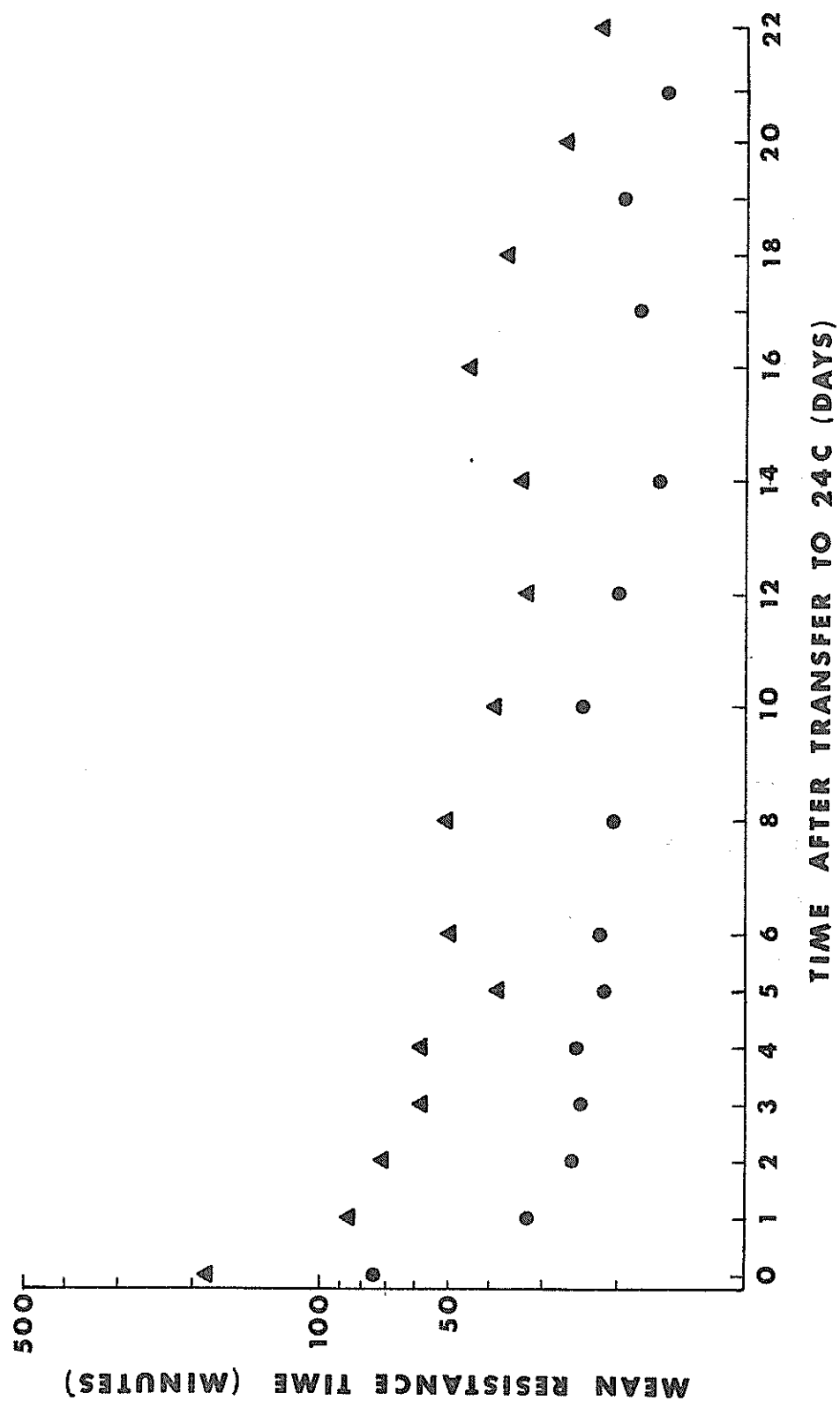


FIGURE 45.--A comparison of the mean thermal resistance times of white (Δ) and brown (\circ) shrimp postlarvae acclimated at 29 C and transferred to 24 C.

FIGURE 45

129



significant interaction between species and time after transfer. This would also seem to indicate that both species responded to a 5 C decrease in temperature in a similar manner.

Seasonal Comparison

The brown shrimp postlarvae tested in September completed their initial acclimation to a temperature increase in approximately the same period of time (3 days) as did the brown shrimp postlarvae tested in April. Therefore, season seems to have had little effect on the acclimation rate of brown shrimp.

Temperature-Salinity Experiments

Brown Shrimp Postlarvae (High Salinity Range)

The individual resistance times of brown shrimp postlarvae acclimated at 29 C and 25, 35 and 45 ppt and tested at 38.2 and 39.0 C and 25, 35, and 45 ppt are shown in Figures 46 and 47. Individual resistance times of brown shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.0 and 39.8 C and 25, 35, and 45 ppt are shown in Figures 48 and 49. The mean resistance times of these brown shrimp postlarvae at each of the six combinations of three acclimation salinities and three test salinities at each acclimation temperature-lethal temperature combination are compared in Figures 50-53. The two replications are combined in the above figures because statistical analysis indicated that there were no significant differences between replications.

FIGURE 46.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 38.2 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 46

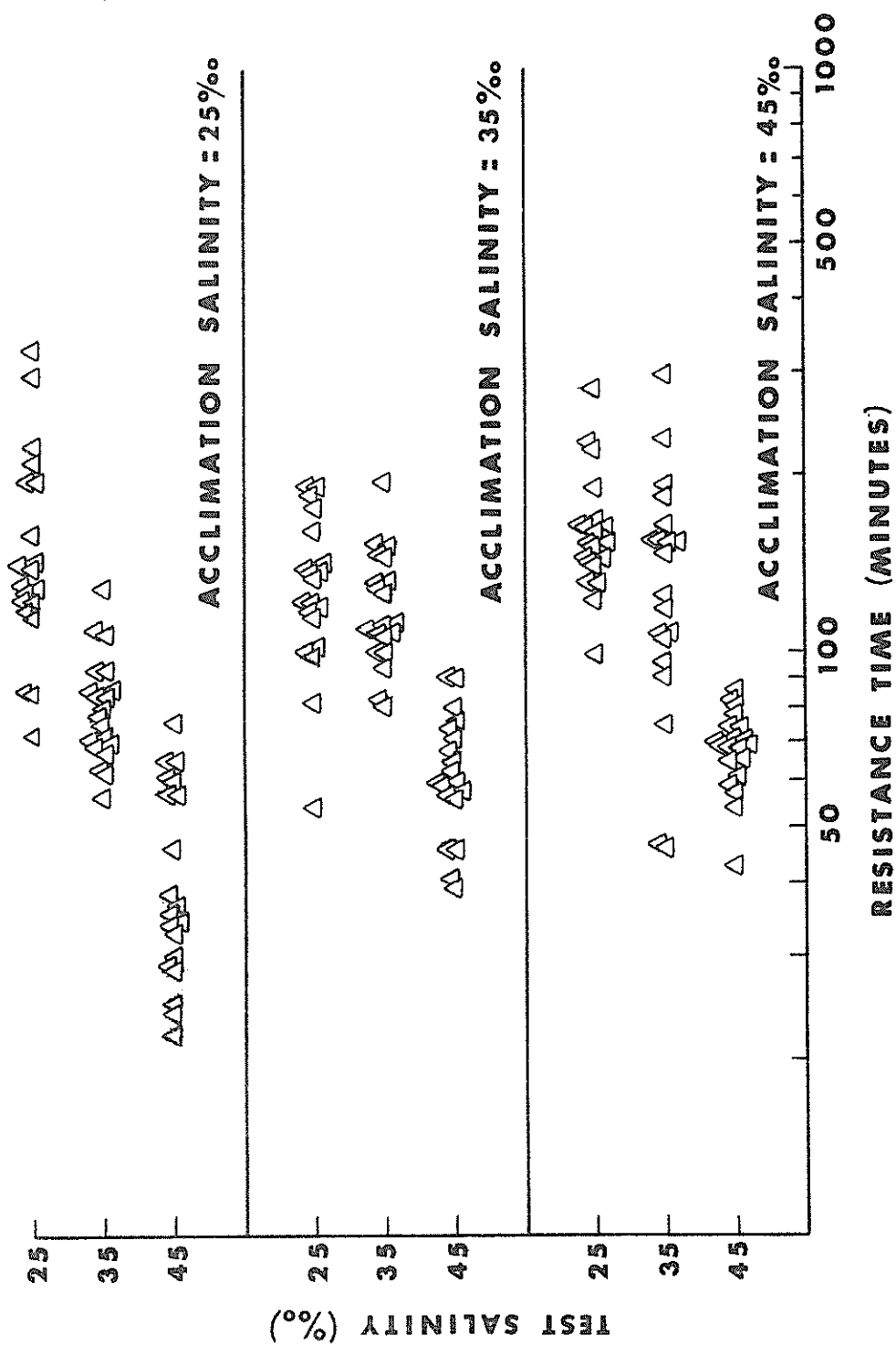


FIGURE 47.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 39.0 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 47

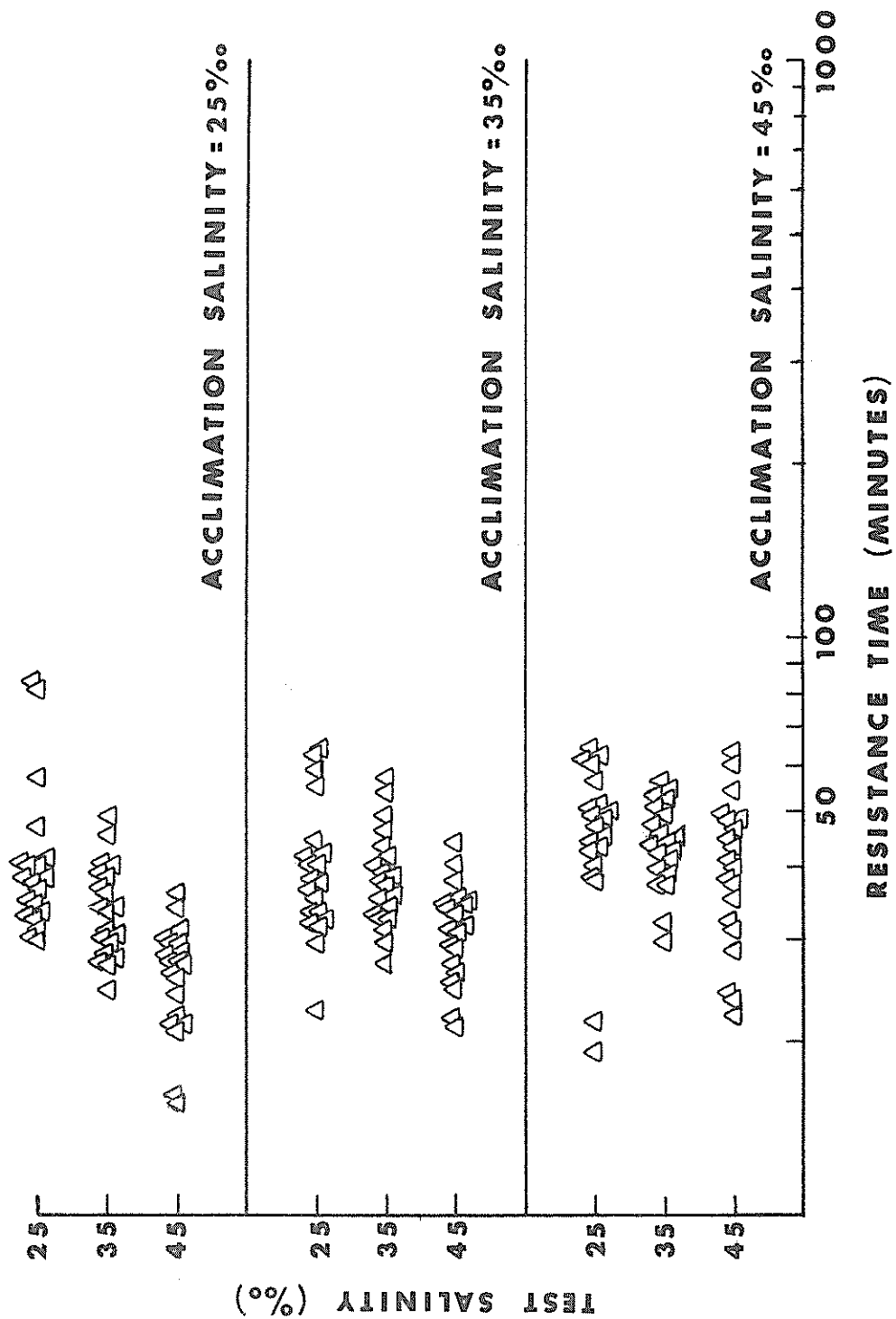


FIGURE 48.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.0 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 48

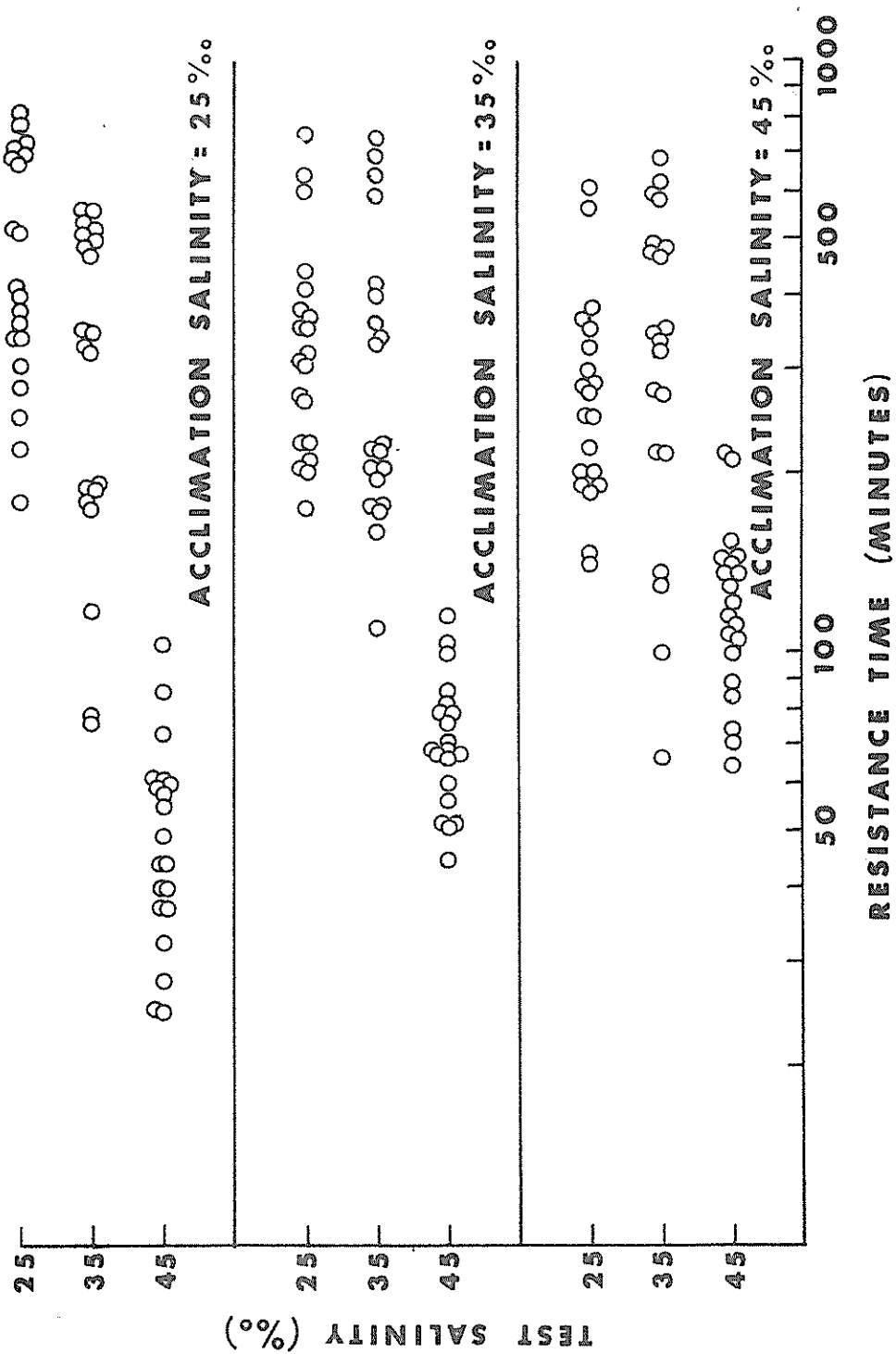


FIGURE 49.--Individual thermal resistance times of brown shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.8 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 49

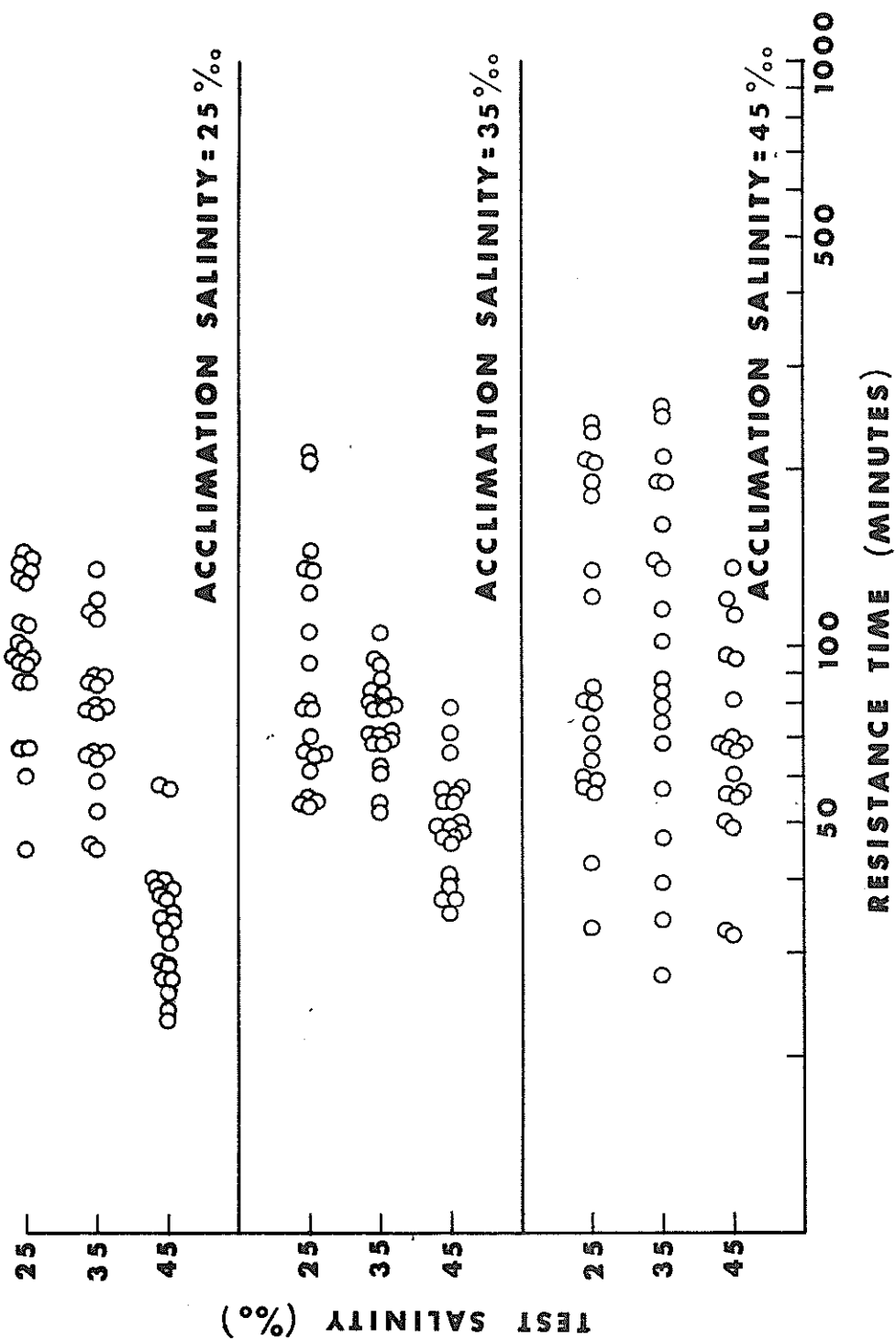


FIGURE 50.--Mean thermal resistance times of brown shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 38.2 C and 25, 35, and 45 ppt.

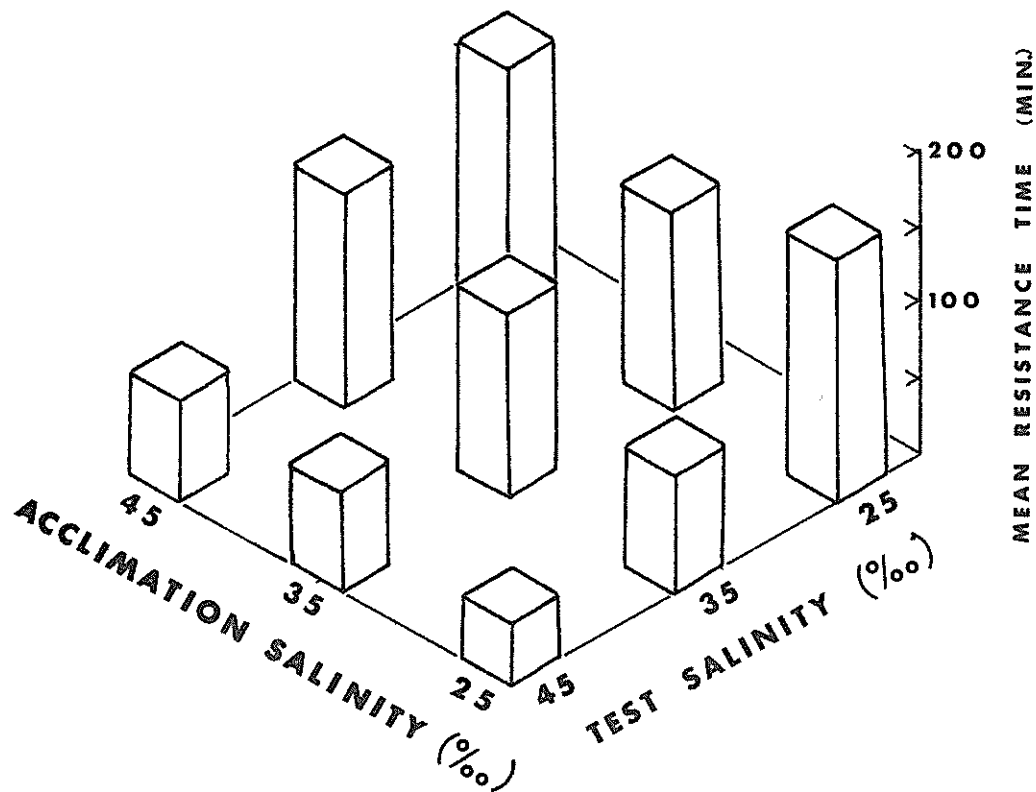


FIGURE 51.--Mean thermal resistance times of brown shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 39.0 C and 25, 35, and 45 ppt.

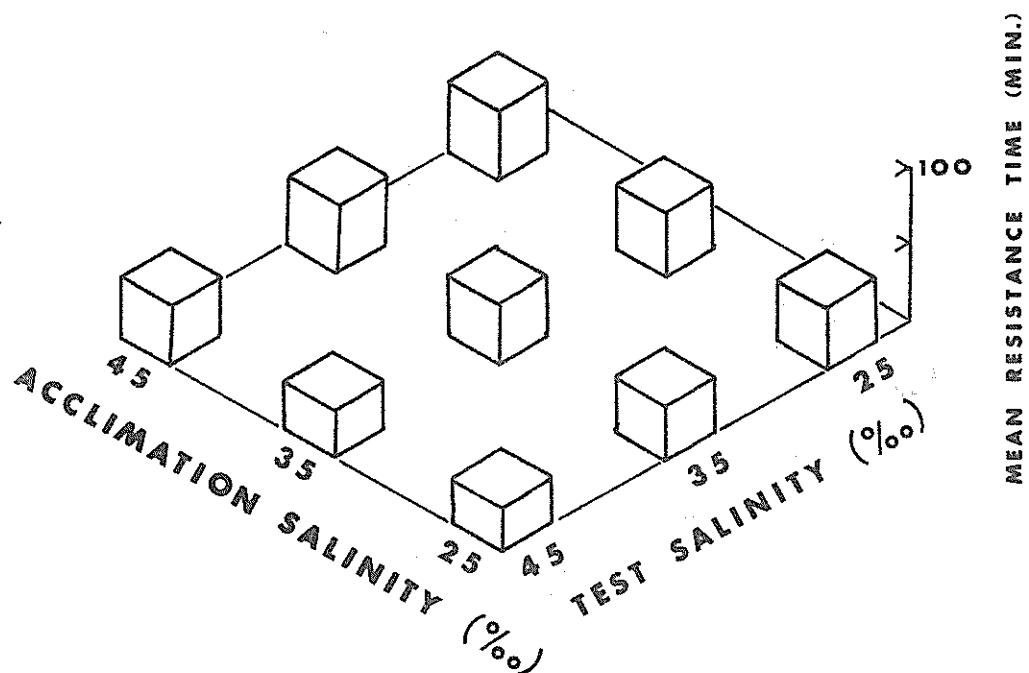


FIGURE 52.--Mean thermal resistance times of brown shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.0 C and 25, 35, and 45 ppt.

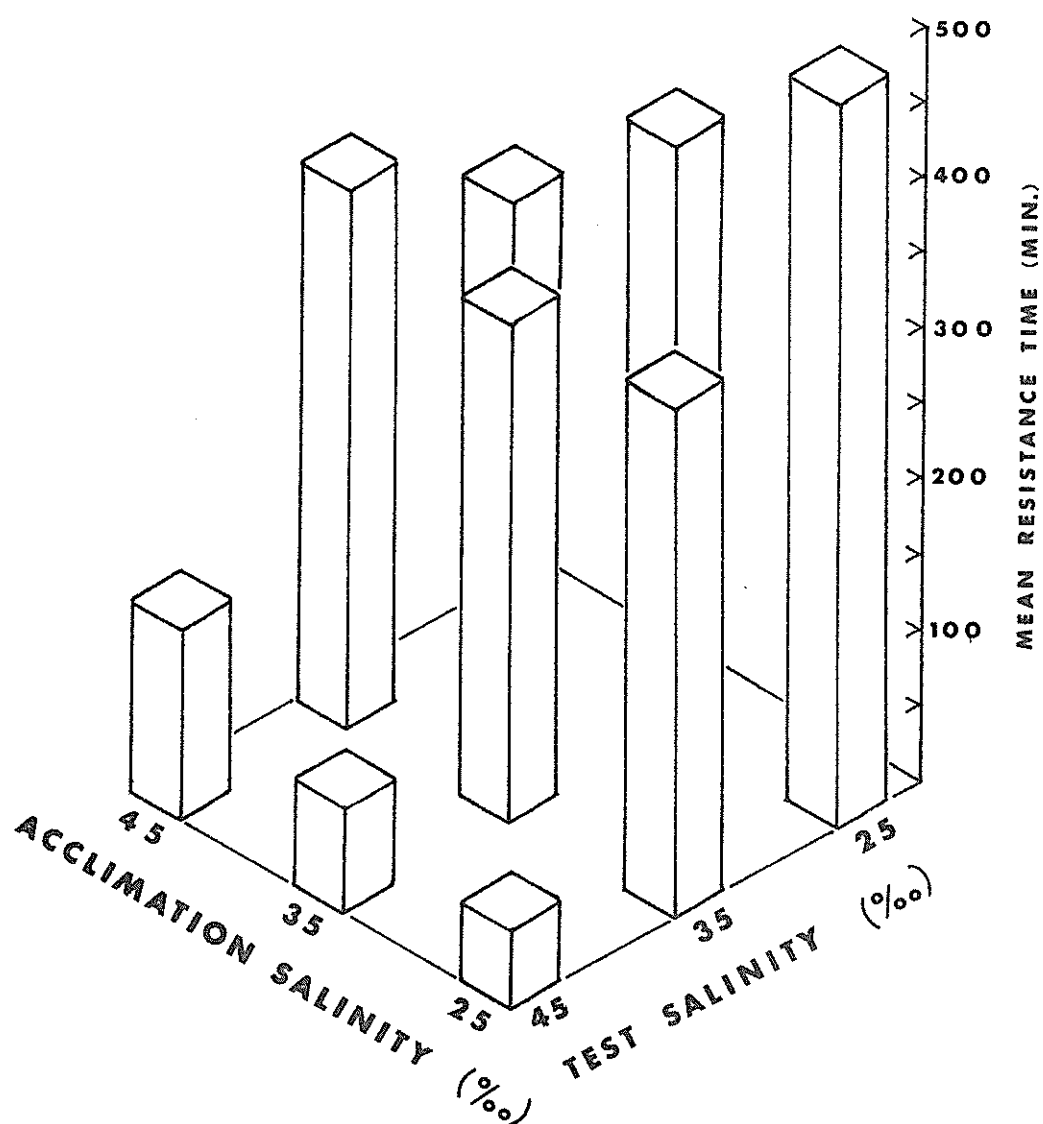
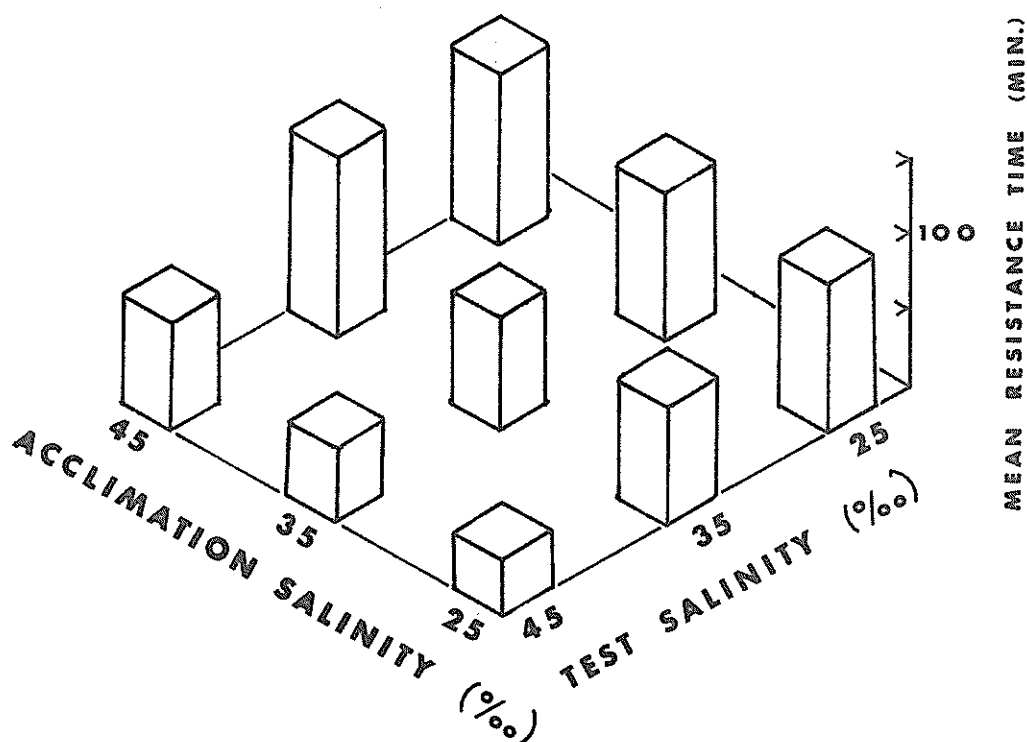


FIGURE 53.--Mean thermal resistance times of brown shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.8 C and 25, 35, and 45 ppt.



A previous study of the effects of temperature and salinity on brown shrimp postlarvae (Wiesepape et al., 1972) found that postlarvae acclimated and tested at a low range of salinities (5, 15, and 25 ppt) were best able to resist lethal temperatures at a test salinity of 25 ppt. However, acclimation to 5 ppt proved to be the best preparation for thermal resistance at all three test salinities.

In the present study, brown shrimp postlarvae acclimated and tested at a higher range of salinities (25, 35, and 45 ppt) were also best able to resist lethal temperatures at a test salinity of 25 ppt (Fig. 50, 51, 52, and 53). Thermal resistance generally increased with decreasing test salinity for each acclimation temperature-salinity combination (Fig. 50, 51, 52, and 53). The postlarvae acclimated at 34 C and 45 ppt were an exception to the above statements. Postlarvae acclimated at that temperature-salinity combination had greater thermal resistance at a test salinity of 35 ppt than they did at 25 or 45 ppt (Fig. 52, and 53). The differences between resistance times at different test salinities were statistically significant, with two exceptions. One of these was for postlarvae acclimated at 34 C and 45 ppt and tested at 39.8 C. This may have been due to the fact that thermal resistance at test salinities of 35 and 45 ppt were similar (Fig. 53). The other non-significant difference in test salinities was for postlarvae acclimated at 29 C and 45 ppt and tested at 39.0 C. The short resistance times at this lethal temperature, which reduced the differences between test salinities, and the increased thermal resistance of postlarvae acclimated at 45 ppt might explain the lack of significance

(Fig. 51).

In general, acclimation at 45 ppt proved to be the best preparation for thermal resistance at all of the test salinities used in this study (Fig. 50, 51, 52 and 53). At a test salinity of 45 ppt, postlarvae acclimated at 45 ppt always were more resistant than postlarvae acclimated at 25 or 35 ppt (Fig. 50, 51, 52, and 53). These differences were found to be statistically significant. At a test salinity of 35 ppt, postlarvae acclimated at 45 ppt had thermal resistance times equal to or greater than those of postlarvae acclimated at 25 or 35 ppt (Fig. 50, 51, 52, and 53). At a test salinity of 25 ppt, the resistance times of postlarvae acclimated at 45 ppt were similar to those of postlarvae acclimated at 25 and 35 ppt, with one exception (Fig. 50, 51, 52, and 53). In the postlarvae acclimated at 34 C and tested at 39.0 C and 25 ppt, those acclimated at 45 ppt had shorter resistance times than those acclimated at 25 and 35 ppt (Fig. 52).

Postlarvae acclimated at 35 ppt generally had thermal resistance times equal to or greater than those of postlarvae acclimated at 25 ppt at test salinities of 35 and 45 ppt (Fig. 50, 51, 52, and 53). At a test salinity of 25 ppt, postlarvae acclimated at 35 ppt were somewhat less resistant than postlarvae acclimated at 25 ppt (Fig. 50, 51, 52, and 53).

There were always statistically significant differences between the two lethal temperatures at each of the acclimation temperatures. However, the differences in resistance time between different lethal temperatures varied with the test salinity, as indicated by the

significant interaction of lethal temperature and test salinity. One result of this interaction was that postlarvae tested at 25 and 35 ppt gained more from a decrease in lethal temperature than did postlarvae tested at 45 ppt (Fig. 50, 51, 52, and 53). There were no significant interactions between acclimation salinity and lethal temperature.

While the acclimation temperatures were not compared statistically, there appear to be differences in the effects of salinity at different acclimation temperatures. For example, postlarvae acclimated at 34 C and 45 ppt did better at a test salinity of 35 ppt than did postlarvae acclimated at 29 C and 45 ppt at the same test salinity (Fig. 50, 51, 52, and 53).

White Shrimp Postlarvae (Low Salinity Range)

The individual resistance times of white shrimp postlarvae acclimated at 29 C and 5, 15, and 25 ppt and tested at 38.5 and 39.0 C and 5, 15, and 25 ppt are shown in Figures 54 and 55. Individual resistance times of white shrimp postlarvae acclimated at 34 C and 5, 15, and 25 ppt and tested at 39.5 and 40.0 C and 5, 15, and 25 ppt are shown in Figures 56 and 57. The mean resistance times of these white shrimp postlarvae at each of the six combinations of three acclimation salinities and three test salinities at each acclimation temperature-lethal temperature combination are compared in Figures 58-61. The two replications are combined in the above figures

FIGURE 54.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C and 5, 15, and 25 ppt and tested at 38.5 C and 5, 15, and 25 ppt. There were 20 shrimp per test.

FIGURE 54

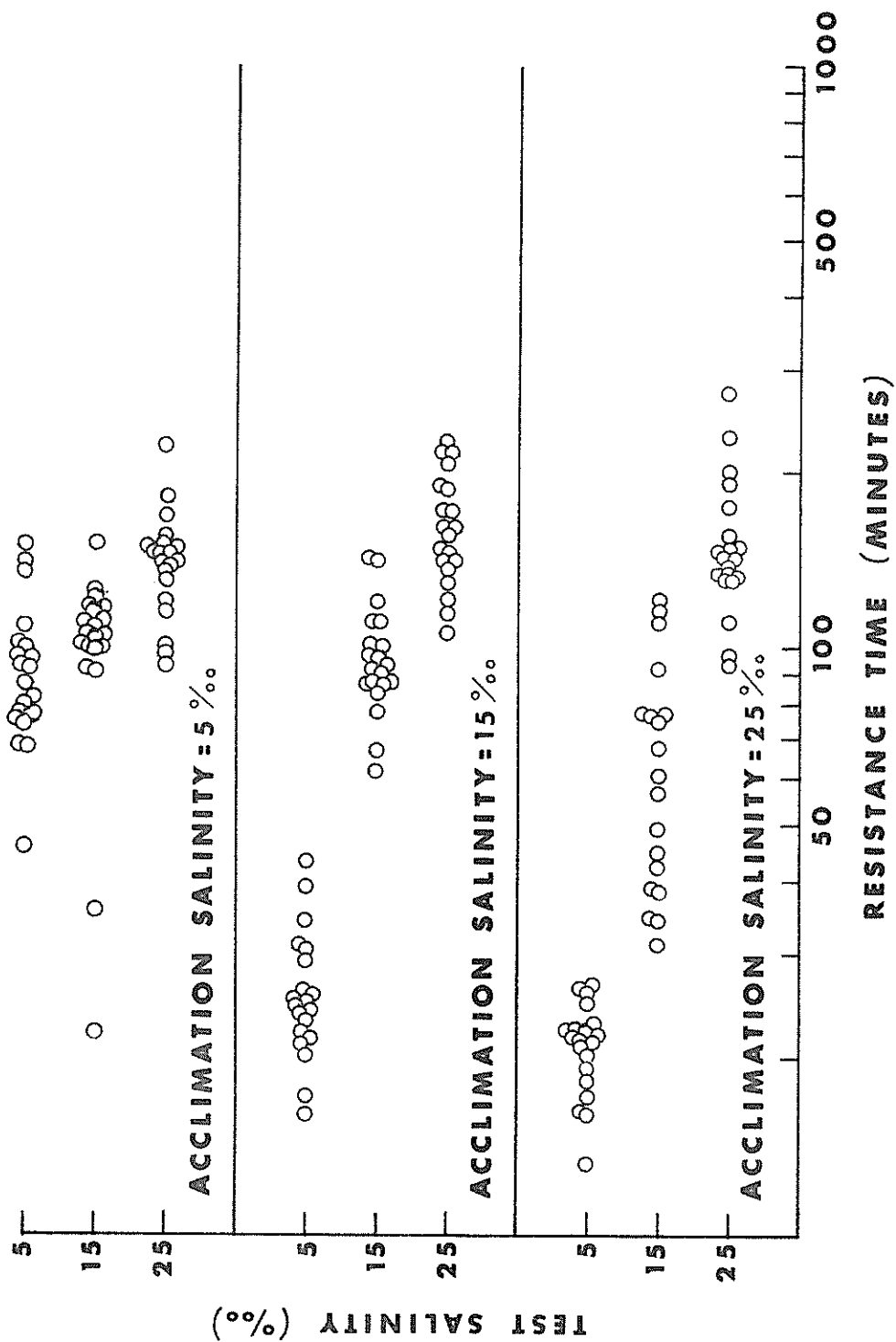


FIGURE 55.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C and 5, 15, and 25 ppt and tested at 39.0 C and 5, 15, and 25 ppt. There were 20 shrimp per test.

FIGURE 55

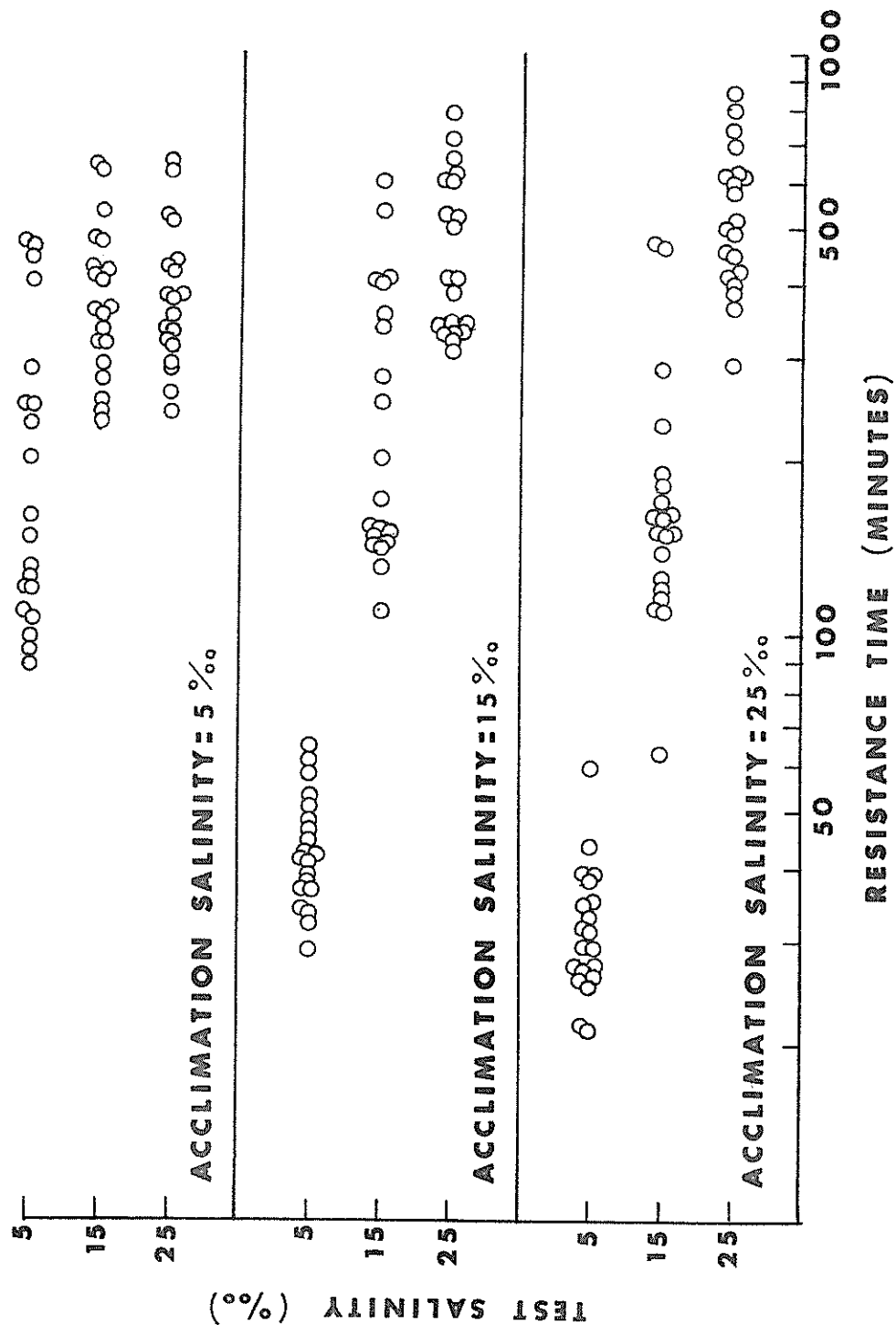


FIGURE 56.--Individual thermal resistance times of white shrimp postlarvae acclimated at 34 C and 5, 15, and 25 ppt and tested at 39.5 C and 5, 15, and 25 ppt. There were 20 shrimp per test.

FIGURE 56

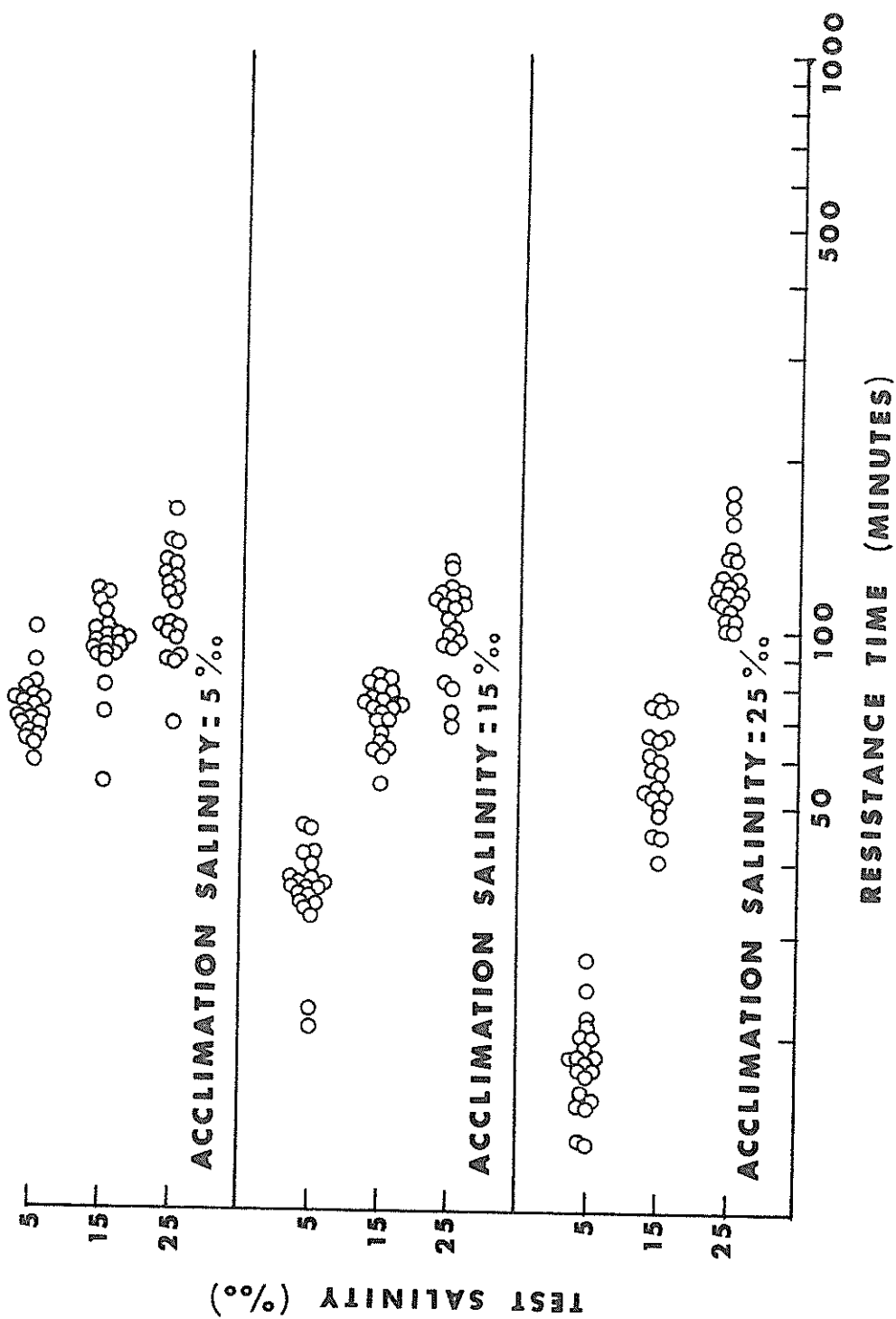


FIGURE 57.--Individual thermal resistance times of white shrimp postlarvae acclimated at 34 C and 5, 15, and 25 ppt and tested at 40.0 C and 5, 15, and 25 ppt. There were 20 shrimp per test.

FIGURE 57

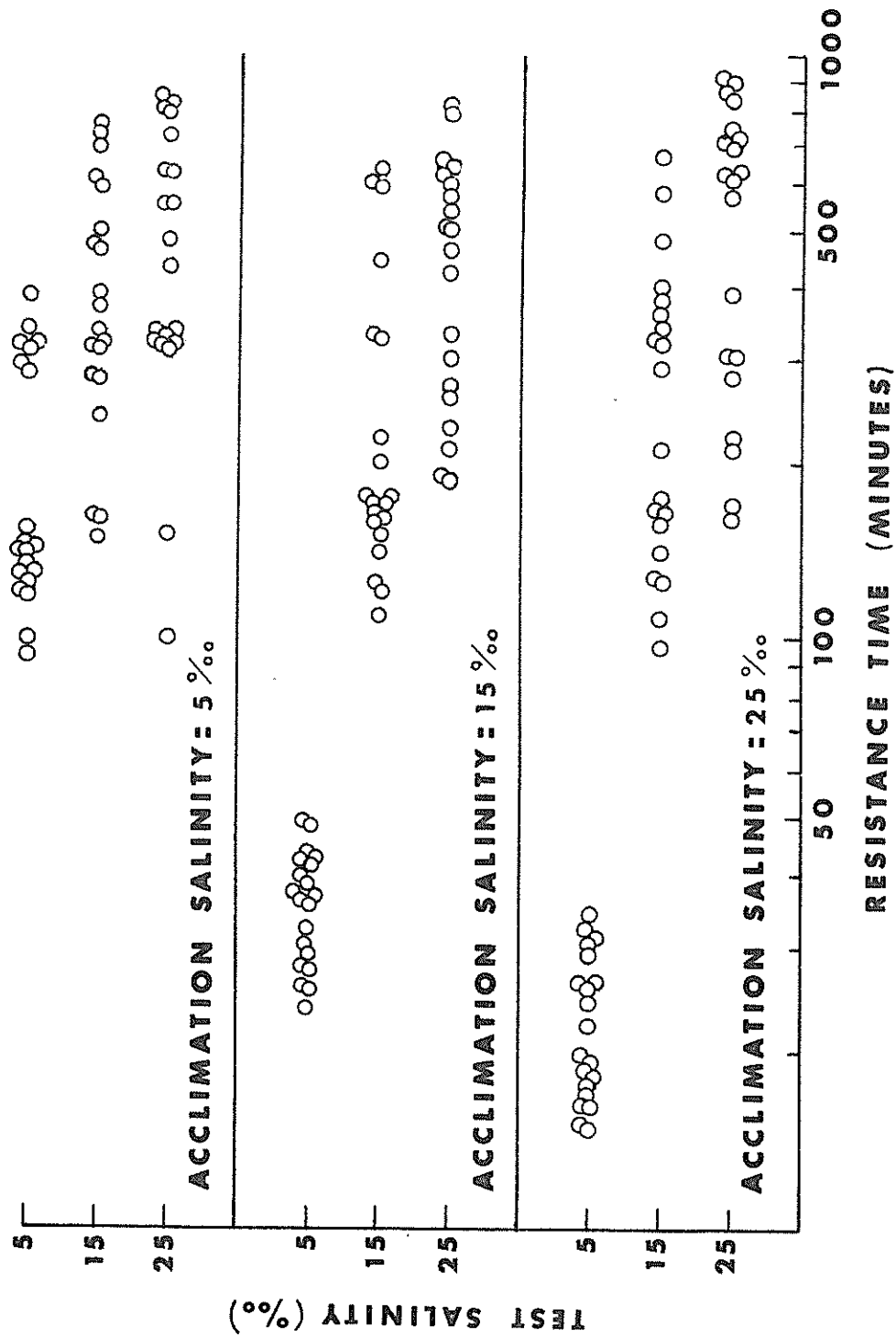


FIGURE 58.--Mean thermal resistance times of white shrimp postlarvae acclimated at 29 C and 5, 15, and 25 ppt and tested at 38.5 C and 5, 15, and 25 ppt.

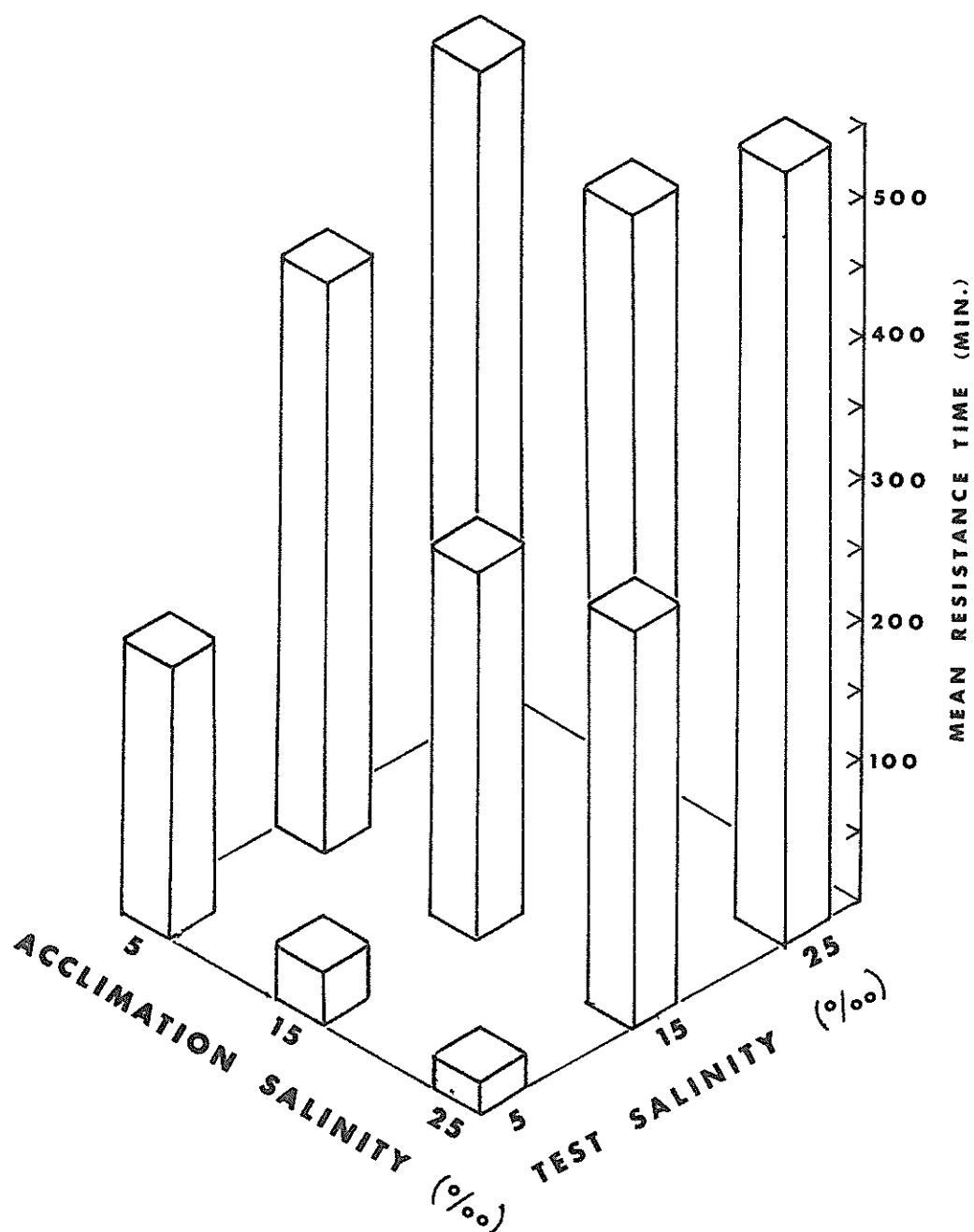


FIGURE 59.--Mean thermal resistance times of white shrimp postlarvae acclimated at 29 C and 5, 15, and 25 ppt and tested at 39.0 C and 5, 15, and 25 ppt.

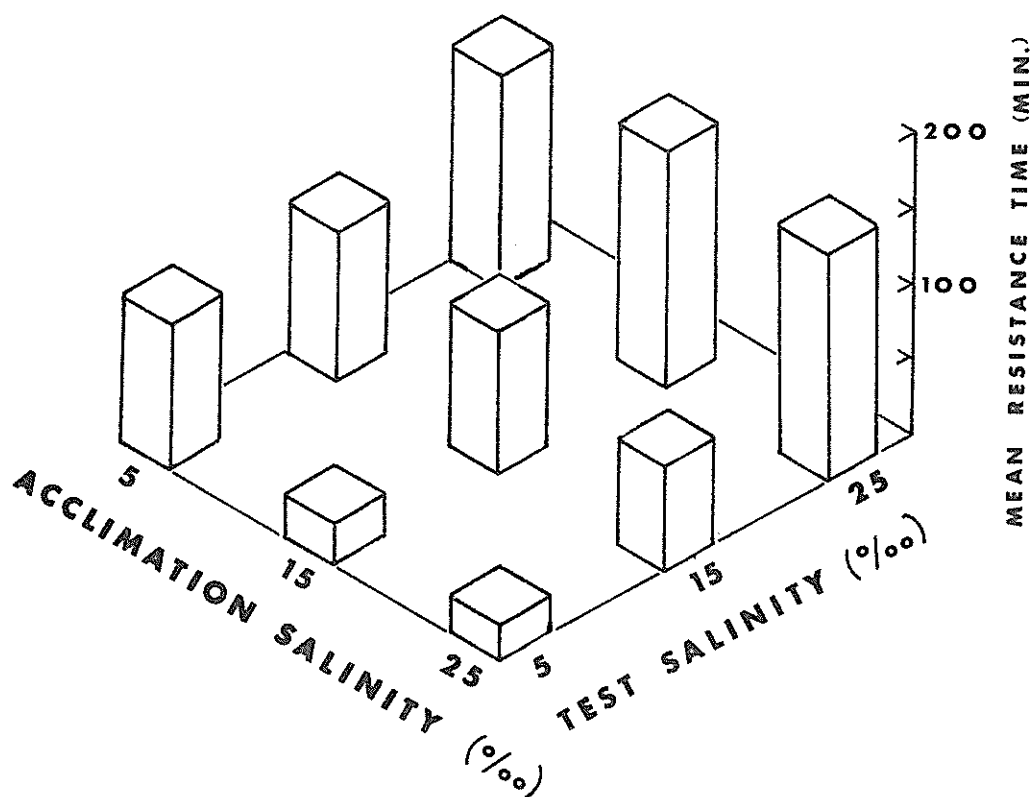


FIGURE 60.--Mean thermal resistance times of white shrimp postlarvae acclimated at 34 C and 5, 15, and 25 ppt and tested at 39.5 C and 5, 15, and 25 ppt.

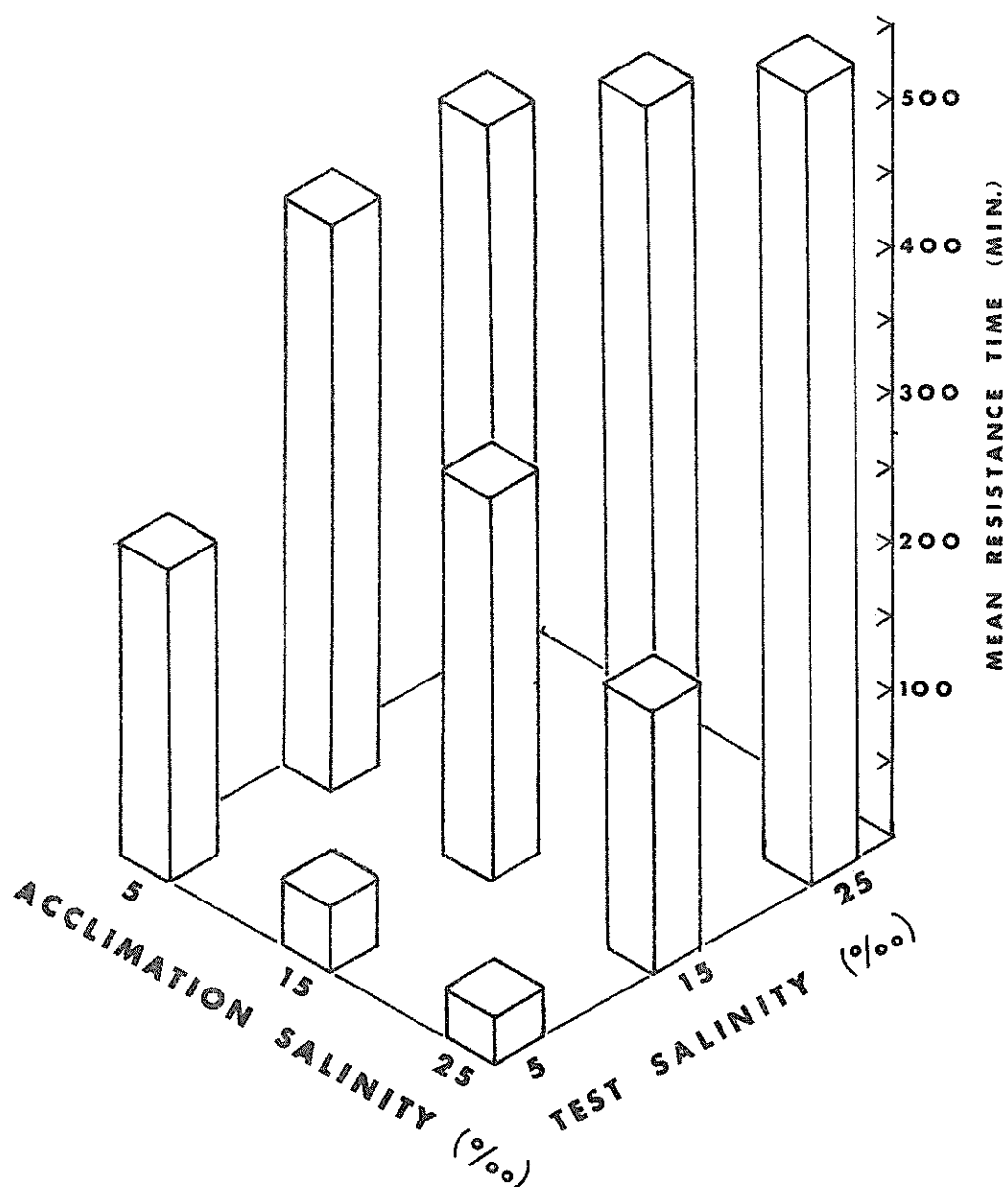
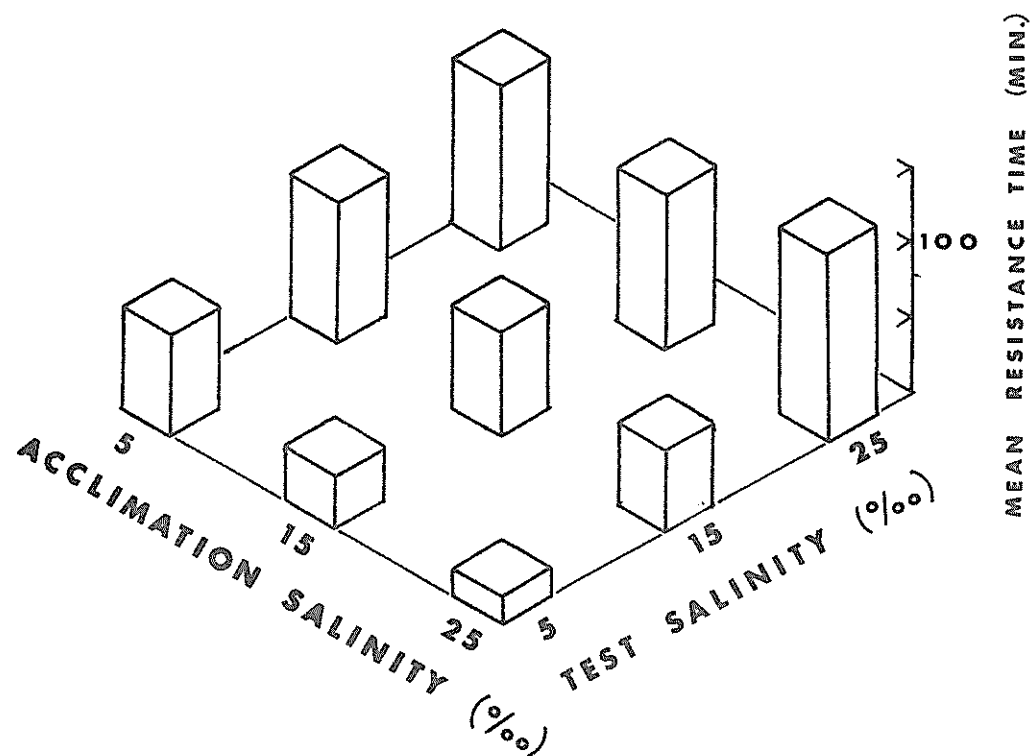


FIGURE 61.--Mean thermal resistance times of white shrimp postlarvae acclimated at 34 C and 5, 15, and 25 ppt and tested at 40.0 C and 5, 15, and 25 ppt.



because statistical analysis indicated that there were no statistically significant differences between replications.

White shrimp postlarvae acclimated and tested at the low range of salinities (5,15 and 25 ppt) were generally affected by these salinities in the same manner as were the brown shrimp postlarvae tested by Wiesepape et al. (1972). Thermal resistance was always greatest at a test salinity of 25 ppt, no matter what the acclimation salinity (Fig. 58, 59, 60 and 61). Thermal resistance also decreased with decreasing test salinity in white shrimp postlarvae, being shortest at a test salinity of 5 ppt for postlarvae from all three acclimation salinities (Fig. 58, 59, 60 and 61). The differences in thermal resistance between test salinities were found to be statistically significant at all levels of acclimation temperature and salinity and lethal temperature.

Acclimation to 5 ppt generally proved to be the best preparation for thermal resistance at any test salinity in white shrimp postlarvae (Fig. 58, 59, 60 and 61). At test salinities of 5 and 15 ppt, postlarvae acclimated at 5 ppt were more resistant than were postlarvae acclimated at 15 or 25 ppt (Fig. 58, 59, 60 and 61). At a test salinity of 25 ppt, postlarvae acclimated at 5 ppt were usually as resistant as postlarvae acclimated at 15 and 25 ppt (Fig. 58, 59, and 61). At a lethal temperature of 39.5 C, postlarvae acclimated at 5 ppt were somewhat less resistant than postlarvae acclimated at 15 and 25 ppt (Fig. 60).

Postlarvae acclimated at 15 ppt were more resistant than postlarvae

acclimated at 25 ppt at test salinities of 5 and 15 ppt (Fig. 58, 59, 60, and 61). At a test salinity of 25 ppt, postlarvae acclimated at 15 ppt had resistance times which were equal to or slightly shorter than the resistance times of postlarvae acclimated at 25 ppt (Fig. 58, 59, 60, and 61).

Statistical analysis indicated that there were no significant differences in the resistance times of postlarvae acclimated at 29 C and tested at 25 ppt. The differences between postlarvae acclimated at 34 C and tested at 25 ppt were significant.

In white shrimp postlarvae, resistance time usually increased with decreasing lethal temperature, and these differences were usually statistically significant. The benefits of a decrease in lethal temperature were much greater at test salinities of 15 and 25 ppt than at 5 ppt (Fig. 58, 59, 60, and 61). In fact, postlarvae acclimated at 29 C and 25 ppt and tested at 5 ppt did not show a statistically significant increase in resistance time with a 0.5 C decrease in lethal temperature.

The two-way interactions between lethal temperature and test salinity were all significant. This also indicates that thermal resistance at a given test salinity was affected by the lethal temperature and, conversely, that thermal resistance at a given lethal temperature was affected by the level of test salinity. The interactions between lethal temperature and acclimation salinity were also significant, except at 29 C acclimation temperature and 25 ppt test salinity. The two-way interactions between acclimation salinity and test salinity

were also significant.

White Shrimp Postlarvae (High Salinity Range)

The individual resistance times of white shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 38.5 and 39.0 C and 25, 35, and 45 ppt are shown in Figures 62 and 63. Individual resistance times of white shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.5 and 40.0 C and 25, 35, and 45 ppt are shown in Figures 64 and 65. The mean resistance times of these white shrimp postlarvae at each of the six combinations of three acclimation salinities and three test salinities at each acclimation temperature-lethal temperature combination are compared in Figures 66-69. The two replications are combined in the above figures because statistical analysis indicated that there were no significant differences between replications.

White shrimp postlarvae acclimated and tested at this high range of salinities (25, 35, and 45 ppt) were generally affected by these salinities in the same manner as were the brown shrimp postlarvae (see above). White shrimp postlarvae were usually most resistant to lethal temperatures at a test salinity of 25 ppt (Fig. 66, 67, 68, and 69). Thermal resistance generally increased with decreasing test salinity for each acclimation temperature-salinity combination (Fig. 66, 67, 68, and 69). Postlarvae acclimated at 29 C and tested at 38.5 C were an exception. Postlarvae acclimated and tested at those temperatures had greater thermal resistance times

FIGURE 62.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 38.5 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 62

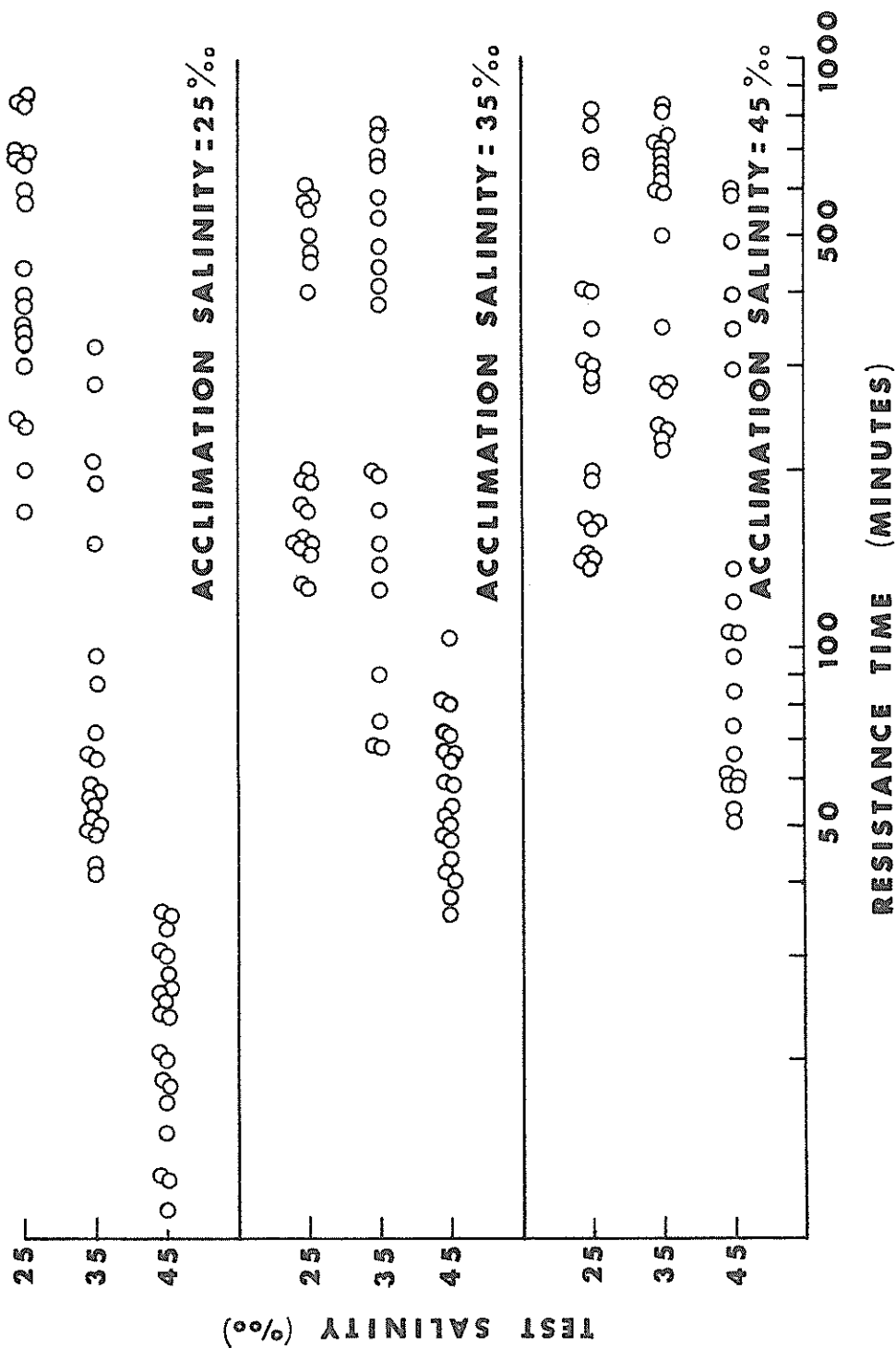


FIGURE 63.--Individual thermal resistance times of white shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 39.0 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 63

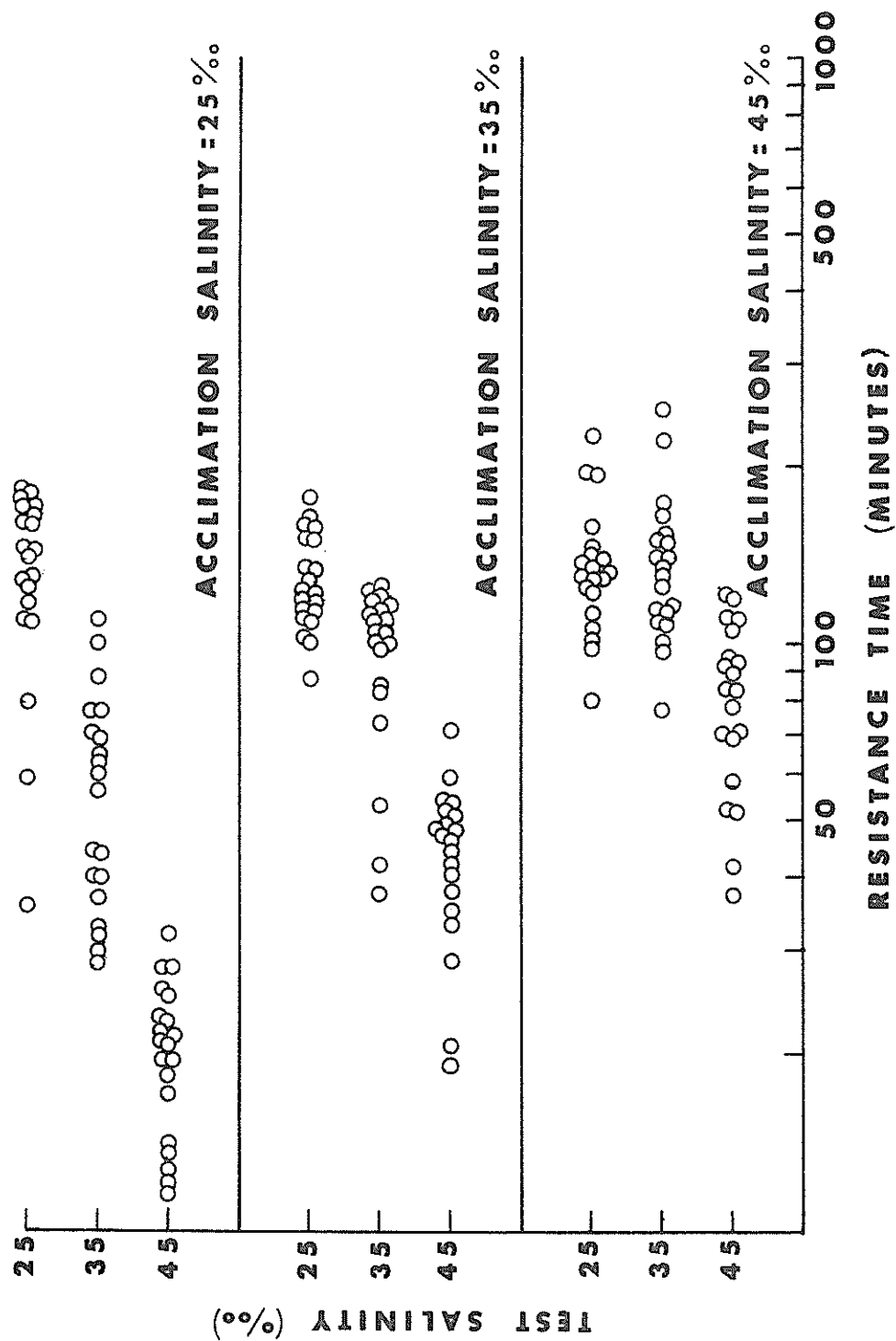


FIGURE 64.--Individual thermal resistance times of white shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.5 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 64

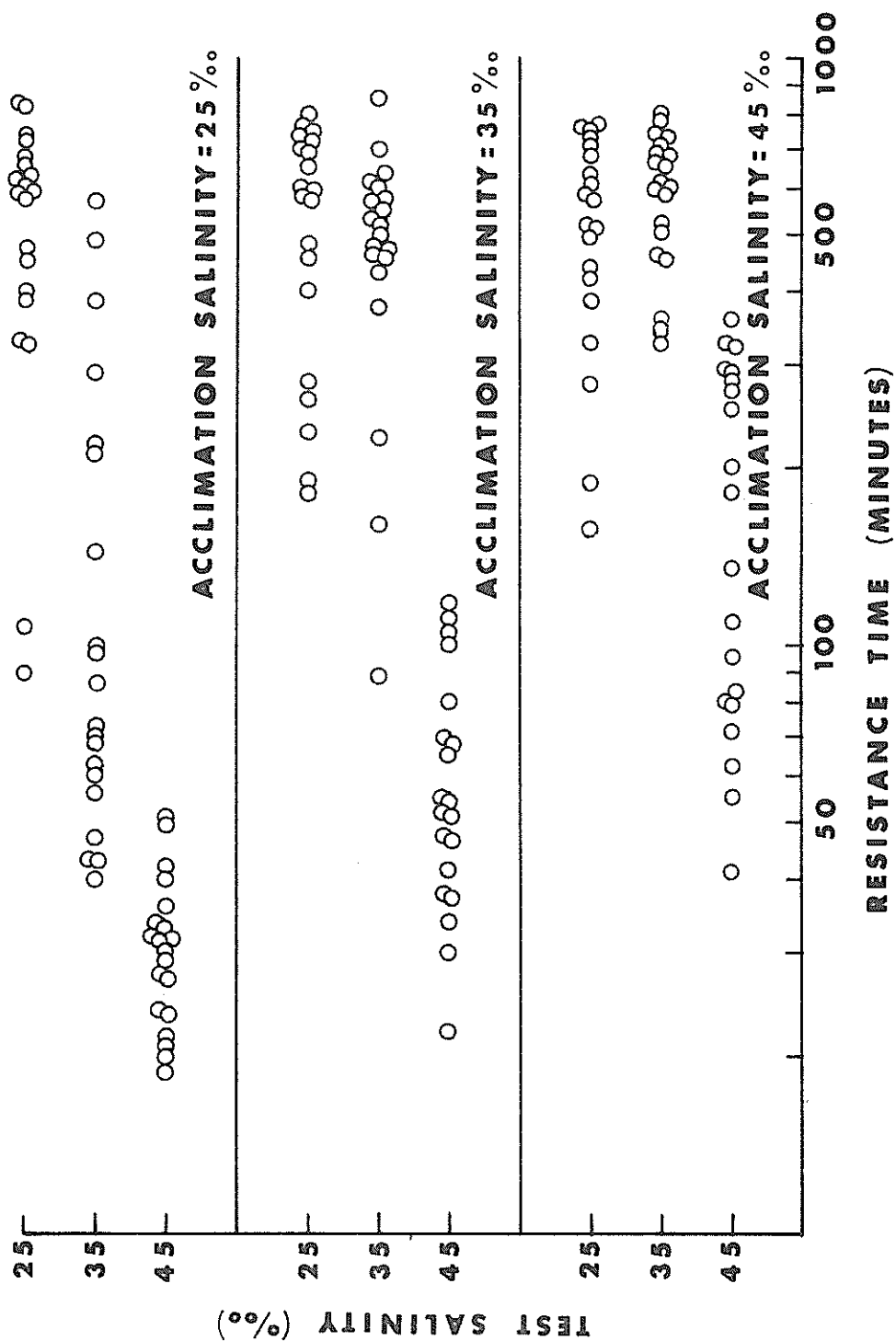


FIGURE 65.--Individual thermal resistance times of white shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 40.0 C and 25, 35, and 45 ppt. There were 20 shrimp per test.

FIGURE 65

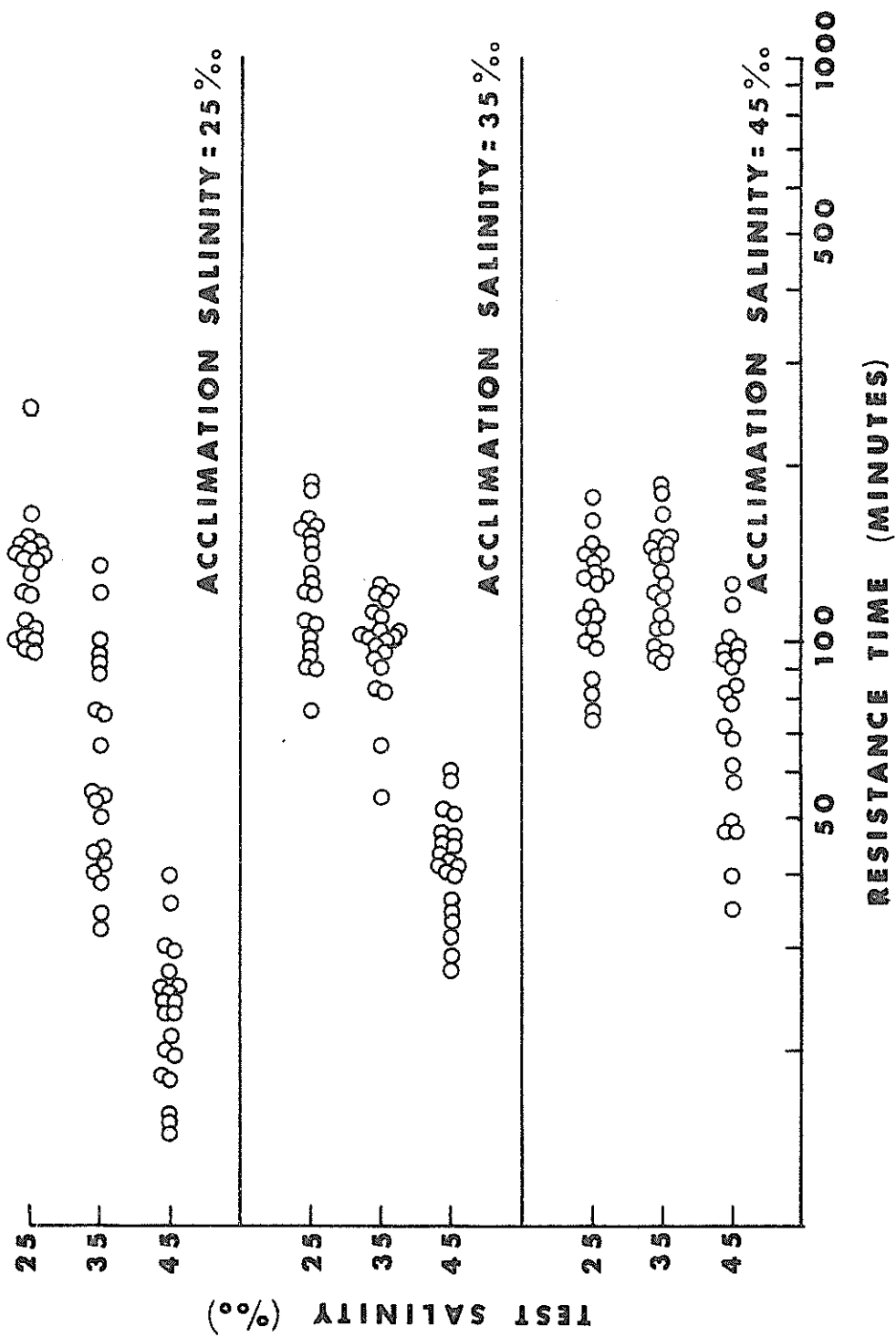


FIGURE 66.--Mean thermal resistance times of white shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 38.5 C and 25, 35, and 45 ppt.

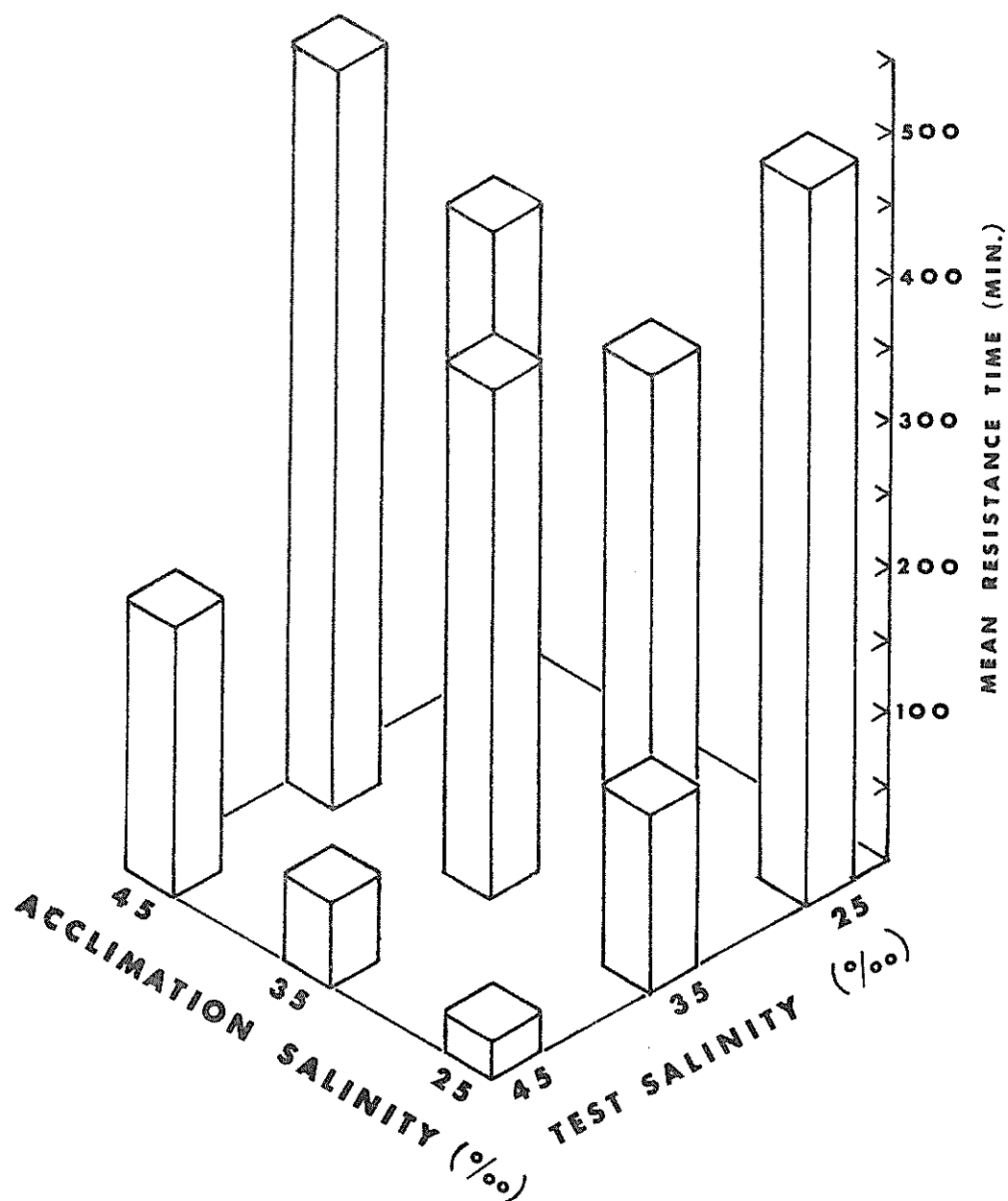


FIGURE 67.--Mean thermal resistance times of white shrimp postlarvae acclimated at 29 C and 25, 35, and 45 ppt and tested at 39.0 C and 25, 35, and 45 ppt.

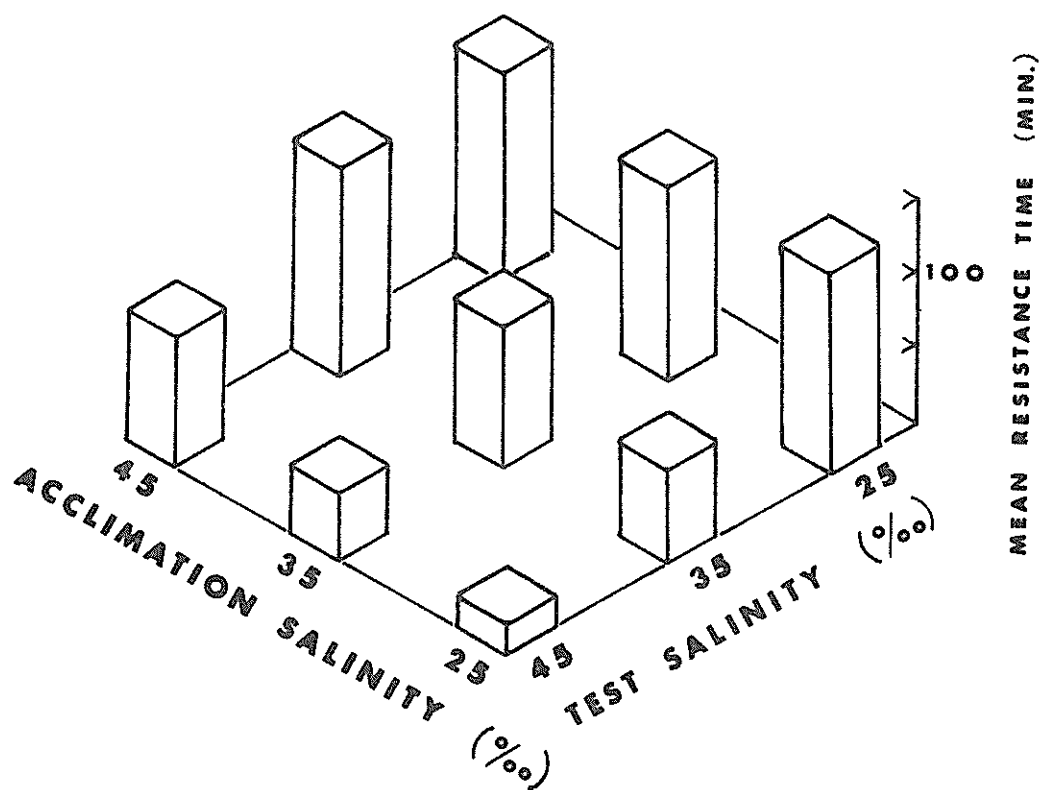


FIGURE 68.--Mean thermal resistance times of white shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 39.5 C and 25, 35, and 45 ppt.

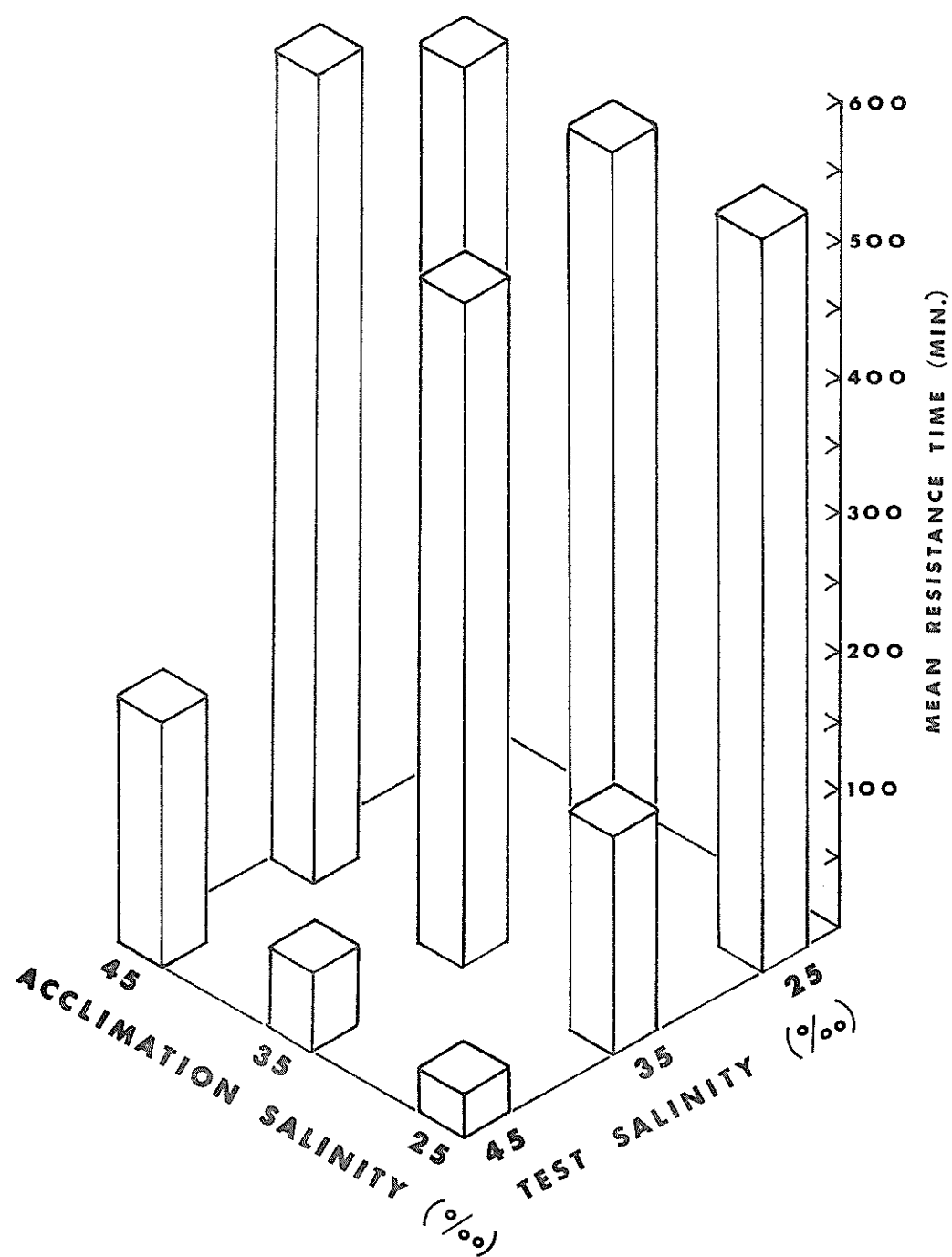
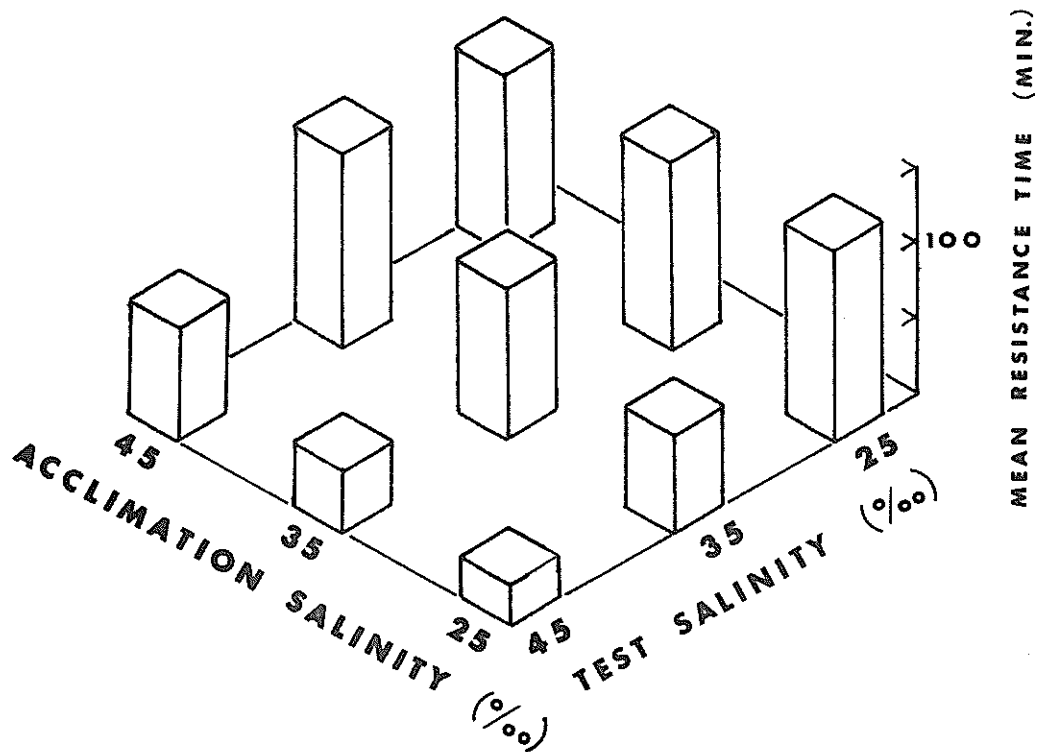


FIGURE 69.--Mean thermal resistance times of white shrimp postlarvae acclimated at 34 C and 25, 35, and 45 ppt and tested at 40.0 C and 25, 35, and 45 ppt.



at a test salinity of 35 ppt when acclimated at 35 and 45 ppt (Fig. 66). The differences between test salinities were always statistically significant at all levels of acclimation temperature and salinity and lethal temperature.

In general, acclimation at 45 ppt again proved to be the best preparation for thermal resistance at all of the test salinities (Fig. 66, 67, 68, and 69). White shrimp postlarvae acclimated at 45 ppt had much greater thermal resistance times at test salinities of 35 and 45 ppt than did postlarvae acclimated at 25 or 35 ppt (Fig. 66, 67, 68, and 69). These differences were found to be statistically significant. At a test salinity of 25 ppt, the thermal resistance times of postlarvae acclimated at all three salinities were similar, except for postlarvae acclimated at 29 C and tested at 38.5 C (Fig. 66, 67, 68, and 69). At that acclimation temperature-lethal temperature combination, the resistance times of postlarvae acclimated at 25 ppt were greater than those of postlarvae acclimated at 35 or 45 ppt (Fig. 66). The statistical analysis substantiated this observation, the differences between acclimation salinities for postlarvae tested at 25 ppt being non-significant except at 29 C acclimation temperature and 38.5 C lethal temperature.

Postlarvae acclimated at 35 ppt were always more resistant than the postlarvae acclimated at 25 ppt at test salinities of 35 and 45 ppt (Fig. 66, 67, 68, and 69). At a test salinity of 25 ppt, the resistance times of postlarvae acclimated at 35 ppt were very close to those of postlarvae acclimated at 25 ppt, except at 29 C acclimation

temperature and 38.5 C lethal temperature (Fig. 66, 67, 68, and 69).

The resistance times of white shrimp postlarvae in this experiment usually increased with decreasing lethal temperature, and these differences were usually statistically significant. The postlarvae acclimated at 29 C and 25 ppt and tested at 45 ppt were an exception, there being no significant difference between lethal temperatures for postlarvae acclimated and tested at these condition. In fact, the benefits of a decrease in lethal temperature were generally greater at test salinities of 25 and 35 ppt than at 45 ppt (Fig. 66, 67, 68, and 69).

The two-way interactions between lethal temperature and test salinity were all significant, also indicating that the effects of the test salinities were not the same at all lethal temperatures. The two-way interactions between lethal temperature and acclimation salinity were significant at all acclimation temperature-test salinity combinations except 29 C and 45 ppt, and 34 C and 25 ppt. The resistance times of postlarvae acclimated at 34 C and tested at 25 ppt were similar for all acclimation salinities at both lethal temperatures, so the difference in resistance time was due to the effects of the lethal temperature only (Fig. 68, and 69). The resistance times of postlarvae acclimated at 29 C and tested at 45 ppt apparently increased with increasing acclimation salinity in a similar manner at both lethal temperatures (Fig. 66 and 67). The two-way interactions between acclimation salinity and test salinity were all statistically significant.

DISCUSSION

The differences in thermal resistance between brown and white shrimp postlarvae may be correlated with the time of year that they enter the bays. In March and April, when most brown shrimp postlarvae enter Galveston Bay (Baxter and Renfro, 1966), periods of mild, slowly rising temperatures are interspersed with periods of reduced temperature caused by the passage of cold fronts. Thus, brown shrimp postlarvae generally face slowly rising temperatures, and, occasionally, fairly rapid temperature decreases. White shrimp postlarvae, entering in the summer, face warm temperatures, which may on occasion reach fairly high levels. Because both species of postlarvae seek out the shallow margins of the bays (Mock, 1966), they are probably affected by changes in air temperature to a greater extent than organisms in the deeper waters.

The present study has revealed that most brown shrimp postlarvae, which enter the bays mainly in the early spring when bay water temperatures are moderate, have less thermal resistance than white shrimp postlarvae, which enter the bays in the summer when bay water temperatures are high (Fig. 11, p. 58). Some brown shrimp postlarvae enter the bays throughout the summer, but in far fewer numbers than in the early spring. It may be that the differences in thermal resistance between white and brown shrimp are adaptations that allow each species to enter the bays at a time when few shrimp of the other species are present. Because both species use the same nursery areas,

this might allow both to gain maximum benefit from these areas, without competing with each other.

The acclimation rate of each species may also be correlated with the temperature conditions which it encounters when it enters the bays. Because acclimation to an increase in temperature is accomplished much more rapidly than acclimation to a decrease in temperature (1-3 days vs. 22 or more days), it would be beneficial for postlarvae faced with sudden drops in temperature interspersed with periods of warmer, rising temperatures to acclimate slowly to increases in temperature during the warm periods. Thus, a sudden drop in temperature would be less likely to occur after the postlarvae had completed acclimation to a higher temperature, from which they would have greater difficulty readjusting to a lower temperature. Under such conditions, the ability to complete at least a part of acclimation to a reduction in temperature in a short period of time would also be beneficial. Brown shrimp postlarvae appear to be adapted to these conditions, because they acclimate fairly slowly to moderate temperature increases (Fig. 20, p. 77, Fig. 21, p. 79), and complete much of their acclimation to a decrease in temperature fairly rapidly (Fig. 29, p. 96). Thus, brown shrimp postlarvae may be physiologically adapted to face the temperature conditions which they encounter in the early spring, when most of them enter the bays.

If temperatures were generally warm, with periods of very warm temperatures, and with little possibility of major temperature decreases, the ability to acclimate rapidly to an increase in temperature

would be more beneficial than in cold weather. This is apparently the case with white shrimp postlarvae (Fig. 31, p. 101, Fig. 32, p. 104, Fig. 33, p. 106), which enter the bay in the summer when such conditions exist. The ability to complete a part of acclimation to a decrease in temperature in a short period of time might not be of great benefit to the postlarvae under such conditions, but on the other hand, it might not be detrimental. Thus, while white shrimp postlarvae are seldom faced with major temperature decreases, they have the ability to complete part of acclimation to a decrease in temperature in a short period of time (Fig. 39, p. 119). This would not be of benefit to the postlarvae in the summer, but might be useful for postlarvae arriving in the fall, when conditions are roughly similar to those present in the early spring.

Although the time required for acclimation is different in brown and white shrimp, both species acclimate most rapidly during the first few hours after a temperature increase. This might be of benefit in facing short periods of high temperature, such as might occur in shallow waters on clear, warm afternoons in both spring and summer.

The benefits of reduction in thermal resistance in later life stages in both species are not readily apparent. This reduction in thermal resistance may coincide with the movement of the larger shrimp from the margins of the bays into deeper water. It would be interesting to determine whether a further reduction in thermal resistance takes place in adult shrimp, which inhabit the Gulf of Mexico where temperatures are relatively stable.

Thermal resistance in both brown and white shrimp postlarvae seems to be affected by salinity in much the same manner. That is, thermal resistance is greatest at or near the isosmotic salinity of both species (27.6-28.3 ppt), and decreases with variation of salinity above and below the isosmotic salinity range.

In the experiment in which brown shrimp postlarvae were acclimated and tested at the high range of salinities (25, 35, and 45 ppt), the test salinity at which thermal resistance was greatest was 25 ppt, the salinity nearest the isosmotic salinity for the species. In the study reported by Wiesepepe *et al.* (1972), in which brown shrimp postlarvae were acclimated and tested at the low range of salinities (5, 15, and 25 ppt), the test salinity at which thermal resistance was greatest was also 25 ppt. In the low and high range salinity experiments on white shrimp postlarvae, the test salinity at which thermal resistance was greatest in both experiments was again 25 ppt, the salinity nearest the isosmotic salinity for that species.

Shaw (1961b) has postulated that crustaceans have adapted to living in reduced salinities by the development of a low ion permeability of the body and an active ion uptake system. An active ion uptake mechanism is probably the more important factor, as an organism cannot be totally impermeable, and several species of crustaceans have been found to be able to regulate well although they are fairly permeable. For example, *Artemia salina* (Croghan, 1958a), *Carcinus maenas* (Shaw, 1961a), and *Eriocheir sinensis* (Shaw, 1961b) have been found to regulate effectively in brackish waters, although all have relatively

high permeabilities.

Active ion uptake in reduced salinities is common in brackish water crustaceans (Robertson, 1960). The mechanism involved in maintaining a reduced internal osmotic concentration in high salinities in crustaceans is not as well known; however, it is likely that it involves an active excretion of ions by the animal, as is the case with marine teleosts (Robertson, 1960).

These active mechanisms require the expenditure of energy by the organism (Potts, 1954); thus, as the salinity is reduced, more energy is required to maintain the internal concentrations at a high level. The same is probably true for increasing salinities above the isomotic salinity.

McFarland and Lee (1963) found that larger brown shrimp (>100 mm) were isosmotic at salinities of 27.6-28.3 ppt. These shrimp were able to regulate their internal osmotic concentrations to be somewhat hyperosmotic to salinities below 27.6 ppt, and hyposmotic to salinities above 28.3 ppt.

McFarland and Lee (1963) also reported that large white shrimp (>100 mm) were isosmotic at the same salinities (27.6-28.3 ppt) as the brown shrimp. Like brown shrimp, white shrimp were also found to be hyperosmotic to salinities below 27.6 ppt, and hyposmotic to salinities above 28.3 ppt.

Wiesepape et al. (1972) suggested that reduced thermal resistance in brown shrimp postlarvae at test salinities of 5 and 15 ppt was due to the increased work necessary for the postlarvae to maintain

the osmotic difference between its internal concentration and the external medium, assuming that the postlarvae reacted to salinity in the same way as did the 100 mm shrimp. This theory was also proposed by Todd and Dehnel (1960), who did a similar study on two species of grapsoid crab. According to this theory, the work necessary to maintain the osmotic difference increases as the salinity decreases below the isosmotic salinity of the animal and creates an added stress on the animal, reducing its ability to resist lethal temperatures.

Since brown shrimp also osmoregulate at salinities above 28.3 ppt, this theory could also explain the reduced thermal resistance at 35 and 45 ppt, as opposed to 25 ppt. Thus, as the salinity increases above 28.3 ppt, the amount of work required to maintain an internal osmotic concentration less than that of the external medium would also increase. Presumably, this would again create an added stress on the animal, reducing its thermal resistance ability.

White shrimp postlarvae, which have the same isosmotic salinities as brown shrimp, and also regulate their internal osmotic concentrations at salinities above and below these isosmotic levels, could be expected to be affected by different salinities in the same manner as are the brown shrimp postlarvae. This is apparently the case, white shrimp being generally affected by salinities above and below 25 ppt in the same manner as were the brown shrimp postlarvae.

Both species of shrimp seem to have evolved a means of maximizing thermal resistance at high and low salinities by acclimating to either

high or low salinities. This process also maximizes thermal resistance at all salinities between the acclimation salinity and the isosmotic level, as was indicated in the temperature-salinity experiments, where a test salinity farther away from the isosmotic level than the acclimation salinity tended to reduce thermal resistance, while a test salinity closer to the isosmotic level than the acclimation salinity tended to increase thermal resistance.

The theory advanced above to explain differences in thermal resistance at different test salinities may also account for the different effects of acclimation salinities. If the energy required to maintain an internal osmotic concentration different from that of the environment is greater at 5 or 45 ppt than at salinities closer to the isosmotic level, then transfer to a salinity closer to the isosmotic level should reduce the work required to maintain the osmotic difference. Conversely, the work required would be increased for postlarvae acclimated at salinities of 15, 25, or 35 ppt, if they were transferred to a salinity further away from the isosmotic level (for example, from 15 to 5 ppt, or from 35 to 45 ppt). Thus, acclimation at a given salinity could prepare the postlarvae for maximum thermal resistance at all salinities closer to the isosmotic salinity, as well as at the acclimation salinity itself.

It would seem that entry into high or low salinity bays would be detrimental to shrimp in terms of thermal resistance. However, both species utilize bays in which the salinity ranges from that of sea water to fresh water for nursery areas, and both species have been

found at salinities above 45 ppt in Laguna Madre, Texas (sizes not given) (Farfante, 1969). This suggests, as Wiesepepe *et al.* (1972) have pointed out, that other factors such as food, protection from predators, or competitors may be the main reason why the postlarvae enter the bays.

Once in the bays, it would benefit postlarvae to seek out very low (or high) salinities. Then, they would have maximum thermal resistance at that salinity, as well as at all salinities closer to the isosmotic salinity. If the salinity should change, it would probably change in the direction of the isosmotic salinity, and the shrimp would still have maximum thermal resistance.

As Wiesepepe *et al.* (1972) have pointed out, these benefits of acclimation to low salinities are probably an adaptation which allows the postlarvae to enter the bays. The maximization of thermal resistance by acclimation to extremes of salinity would seem to be an adaptation which would allow both species to utilize both high and low salinity bays for nursery areas while minimizing the possibility of heat death. Field studies have indicated that in areas having high salinity bays, such as the lower Texas coast, brown shrimp predominate, while in areas having low salinity bays, such as the Louisiana coast, white shrimp predominate (Gunter, 1954; Parker, 1970). This difference in distribution may be related to the difference in osmoregulatory ability reported by McFarland and Lee (1963), who found that brown shrimp maintained a greater difference between their internal osmotic concentration and the external medium at salinities above the isosmotic

level than they did at salinities below it. White shrimp, on the other hand, maintained a greater difference at salinities below the isosmotic level than they did at salinities above it.

According to the theory advanced above, brown shrimp should have somewhat less thermal resistance at salinities above 28.3 ppt than at salinities below 27.6 ppt, since they would expend more energy at the higher salinities in order to maintain the osmotic difference. Comparison of the results of the present research on thermal resistance in brown shrimp postlarvae at high salinities with those of Wiesepepe *et al.* (1972) on brown shrimp postlarvae at low salinities indicates that this is generally true.

White shrimp, on the other hand, should have somewhat greater thermal resistance at the higher salinities than at the lower salinities. However, a comparison of the experiments conducted with white shrimp postlarvae indicates that thermal resistance is very similar at both high and low salinities. The reason for this similarity is not readily apparent. It is possible that causes other than the work required to maintain an osmotic difference affect the thermal resistance of white (and perhaps also brown) shrimp postlarvae. As Arai, Cox, and Fry (1963) have pointed out, the effects of salinity on thermal resistance are often complex. While expenditure of energy to maintain an osmotic difference seems to explain many of the effects of salinity on thermal resistance, it may not be the only factor involved.

While many differences between white and brown shrimp were found, these experiments also revealed some similarities between the two species. Thus, while acclimation rates to increases in temperature differed between the two species, acclimation to a decrease in temperature did not differ significantly. The overall effects of salinity on thermal resistance were similar in both species. Based on serological comparisons of *Penaeus aztecus* and *P. setiferus*, Leone and Pryor (1952) concluded that the two species are "distinct, but closely related species". The results of the present investigation tend to agree with this conclusion.

The use of bays as sources of cooling water for power plants, and the consequent heating of the water has raised questions about the effects of thermal addition on organisms in the bays. The results of this investigation give some reference points for assessing the effects of thermal additions on brown and white shrimp.

The 24-hour LC_{50} , or "median lethal temperature", is commonly used to define the tolerance limits of organisms when the probable effects of thermal effluents are assessed (Kennedy and Mihursky, 1971). The 24-hour LC_{50} 's of white and brown shrimp postlarvae at each of the acclimation temperatures used in these experiments have been provided (pages 42 and 51). Of course, temperatures somewhat lower than the LC_{50} 's may be lethal with longer exposure times.

It is difficult to give a precise temperature which marks the boundary between lethal and non-lethal temperatures, because thermal resistance is affected by a complex set of variable factors. These

factors determine the exposure time necessary before the death of the organism occurs.

Acclimation temperature can have an important effect on the resistance time of a postlarva at a given temperature. Since the acclimation temperature of shrimp under natural conditions is not known, it is often impossible to predict the exact temperature which will be lethal to a wild shrimp in a given period of time. Further research would help clarify this. Investigation of the thermal resistance of shrimp taken directly from the field and tested at different lethal temperatures, and tests of shrimp acclimated to diurnally variable temperatures, would provide more information on this subject. However, it now should be possible to determine approximate lethal temperatures for shrimp living within the range of acclimation temperatures used in this study.

Salinity, as indicated in the present study, also has an important effect on thermal resistance in both species of shrimp. Thus, heated effluents of a different salinity from that of the receiving area might have either detrimental or beneficial effects on the thermal resistance of brown and white shrimp, depending on the salinities involved. Heated effluents of very high or low salinity discharged into an area of moderate salinity, could drastically reduce the ability of shrimp to resist the increased temperature. On the other hand, heated effluents with a salinity at or near the isosmotic salinity of white and brown shrimp might, on some instances, increase their thermal resistance. This could occur if the salinity of the area

into which the heated effluents were discharged was much higher or lower than the isosmotic salinity of the shrimp.

The results of this investigation provide information which could be useful in the culture of brown and white shrimp. The thermal resistance experiments define the lethal temperatures of each species, which should obviously be avoided in the transfer of shrimp during culture operations.

At non-lethal temperatures, white and brown shrimp can apparently withstand considerable changes in temperature, as long as concurrent changes in salinity do not occur. Changes in both temperature and salinity, however, can have detrimental effects which are not apparent when changes in only one factor occur, as indicated by the temperature-salinity experiments. Temperatures which are not lethal at isosmotic salinities may become so if the shrimp are subjected to a change from isosmotic to much higher or lower salinities at the same time. When large changes in both temperature and salinity are required, it would be wise to allow the shrimp to acclimate to the change in one factor before changing the other factor.

In their investigation of acclimation in *Ictalurus punctatus*, Allen and Strawn (1971) found that there were oscillations in resistance time over the period of the experiments. Similar results were reported for *Cyprinodon variegatus* by Simmons (1971). Similar oscillations in resistance time were also found in the acclimation experiments on brown and white shrimp postlarvae. A regularly recurring

natural event, or an internal rhythm in thermal resistance might be the cause of these fluctuations. The fact that the peaks of thermal resistance do not always occur on the same day in different experiments makes it difficult to match the fluctuations to a rhythmic environmental event. Since temperature, salinity, photoperiod, feed, and time of day of testing were controlled rather closely for each experiment, variations in these factors can probably be ruled out as causes of the fluctuations.

The reasons for these fluctuations in thermal resistance are not readily apparent. However, the presence of this phenomenon in a fish (*Ictalurus punctatus*) and two species of crustacean (*Penaeus aztecus* and *P. setiferus*) indicates that it may be a common characteristic of poikilotherm animals.

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